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Three-Dimensionally Preserved Arthropods from the Cambrian (Furongian) of Quebec and Wisconsin: Systematics, Phylogeny, Ichnology, and Taphonomy

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THREE-DIMENSIONALLY PRESERVED ARTHROPODS FROM THE
CAMBRIAN (FURONGIAN) OF QUEBEC AND WISCONSIN: SYSTEMATICS,
PHYLOGENY, ICHNOLOGY, AND TAPHONOMY

A Thesis Presented

by

JOSEPH H. COLLETTE III

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

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Department of Geosciences

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ABSTRACT

THREE-DIMENSIONALLY PRESERVED ARTHROPODS FROM THE CAMBRIAN (FURONGIAN) OF QUEBEC AND WISCONSIN: SYSTEMATICS, PHYLOGENY, ICHNOLOGY, AND TAPHONOMY

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Three new types of arthropod from Cambrian intertidal lithofacies of the Elk Mound Group and Lodi Member of Wisconsin, and the Potsdam Group of Quebec are described. These arthropods are preserved ventrally in three dimensions – allowing detailed characterization of morphology. *Arenocaris inflata*, from the Furongian Elk Mound Group and St. Lawrence Formation, is the earliest occurrence of a phyllocarid. *Mosineia macnaughtoni*, a large (>10 cm long) euthycarcinoid arthropod, also occurs in Elk Mound strata. *Mictomerus melochevillensis* represents a new family of early euthycarcinoids, and is a large (8–10+ cm long) arthropod with eleven pairs of homopodous, uniramous limbs.

Phylogenetic analyses and reviews of Paleozoic phyllocarid systematics are presented, using morphology-based characters from Cambrian to Recent taxa. Resulting cladograms place *Arenocaris inflata* into a systematic context, and reveal that the families Ceratiocarididae and Caryocarididae, as traditionally defined, are paraphyletic. Caryocarididae is elevated to subordinal rank (Caryocaridina n. suborder), resulting in two monophyletic suborders. Emended diagnoses are integrated

into this analysis, and result in synonymy of 30 Cambrian – Silurian caryocaridids and ceratiocaridids into 11 pre-existing species.

The phyllocarid *Arenocaris inflata* from the Elk Mound Group of Wisconsin and the large enigmatic arthropod *Mictomerus melochevillensis* from The Potsdam Group of Quebec are both directly associated with trace fossils. Direct association between these arthropods and their traces allows functional morphological details of the animal to be assessed, provides a framework for understanding how arthropods can be sand-cast in three-dimensions, and helps provide insight about subaerially-produced traces from the Potsdam Group.

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CHAPTER 1.

THREE-DIMENSIONALLY PRESERVED ARTHROPODS FROM CAMBRIAN LAGERSTÄTTEN OF QUEBEC AND WISCONSIN

Introduction

Cambrian intertidal sandstones and orthoquartzites of Laurentia have received increasing attention in recent years because they contain surprising types of soft-bodied fossils, particularly mass strandings of scyphomedusae (Hagadorn et al., 2002a; Collette and Hagadorn, 2008; Hagadorn and Belt, 2008; Lacelle et al., 2008). In addition, spectacularly preserved invertebrate trace fossils also occur in these settings, perhaps mediated by the presence of biomats or biofilms (MacNaughton et al., 2003; York et al., 2005; Hagadorn and Belt, 2008; Seilacher, 2008). Subaqueous fossil trackways include such diverse forms as *Climactichnites*, *Diplichnites*, *Musculopodus*, *Protichnites*, *Teichichnus*-like burrows, and a diverse array of undescribed arthropodan trackways, including phyllocarid surface trails and burrows (Hoxie, 2005; Collette and Hagadorn, 2008). Rarer, subaerially produced arthropodan trace fossils have also been reported from the Elk Mound Group of Wisconsin, and the Potsdam Group of Quebec, Ontario, and northern New York (MacNaughton et al., 2002; Hoxie and Hagadorn, 2005; Collette and Hagadorn, 2008; Hagadorn, 2008).

Until recently, no body fossil evidence existed that could help identify potential producers of the arthropodan trackways in these Lagerstätten. Yet producers of the subaerial trackways may have been aglaspideid- or euthycarcinoid-like arthropods, perhaps making periodic forays onto land (MacNaughton et al., 2002). Herein, new

arthropods are described that sharpen our picture of life in these settings. This new material includes the earliest known occurrence of the Phyllocarida (Crustacea: Malacostraca) with well-preserved limbs, as well as two large, enigmatic euthycarcinoids with a curious mixture of characters. One of these euthycarcinoid arthropods, *Mictomerus melochevillensis* n. sp. has a size, shape, and number of appendages ($n = 11$) suitable to have produced subaerial trackways previously reported from the Potsdam Group by MacNaughton et al. (2002).

What is most striking about these new arthropods is that they are preserved in three-dimensions in fine- to medium-grained quartz arenites. This style of preservation is more typical of Ediacaran fossil deposits (Narbonne, 1998; Hagadorn and Belt, 2008), and is thought to result from microbial binding of sediments (Gehling, 1999). This mode of preservation does not appear to characterize these arthropods, because their preservation is mediated by burial in mud and post-decay casting by sand (Collette and Hagadorn, 2008).

Stratigraphy and Depositional Environments

The specimens described herein were collected in Mosinee, Wisconsin (PRI station number 3421); south of Arcadia, Wisconsin; and Melocheville, Quebec (now part of the city of Beauharnois) (PRI station number 3849). Quartz arenites of the Elk Mound, St. Lawrence, and Potsdam units were deposited on the shores of Laurentia as it lay about 10° south of the equator (Blakey, 2007) (Figure 1A). Mature quartz sands were deposited on the margins of a shallow epicontinental sea, where a very shallow cratonic gradient of 1:10,000 to 1:50,000

likely yielded tidal fetches between 10 and 50+ km (Byers and Dott, 1995; Runkel et al., 1998; Rose and Hagadorn, 2006), and a variety of shallow marine and marginal marine environments persisted. Sedimentary structures, cross-cutting relationships, lithologies, trace fossils, and abundant scyphomedusae fossils in fossil-bearing portions of the Elk Mound and Potsdam Groups indicate similar environments of deposition, in a suite of shallow to emergent wave-dominated tidal flats (Bjerstedt and Erickson 1989; Hagadorn et al., 2002b; Hagadorn and Belt, 2008). Lithologies of the Lodi member of the St. Lawrence Formation, in contrast, are consistent with a shallow offshore setting below fair-weather wave base (Hughes and Hesselbo, 1997). The studied portions of these three units were deposited during Furongian time.

Elk Mound Group

The Elk Mound Group in Wisconsin (Figure 1A, B) rests unconformably on Precambrian igneous and metamorphic basement, and is composed of three units: the Mount Simon, Eau Claire, and Wonewoc Formations. The Mount Simon is comprised of clean, mature quartz arenites. Sedimentary structures and trace fossils indicate fluvial/tidal channel to sand-flat depositional settings (Driese et al., 1981). The Eau Claire Formation consists of fine grained sandstone and siltstone with abundant interstratified shale (Driese et al., 1981). Trilobites, aglaspids, hyolithids, and inarticulate brachiopods occur in this unit (Driese et al., 1981; Hesselbo, 1989). This unit has been interpreted to represent shallow marine shelf (Aswasereelert et al., 2008) to intertidal to shallow sub-tidal deposition (Hughes et al., 1997). The Eau Claire falls between the *Cedaria* – *Crepicephalus* and *Aphelaspis* trilobite zones, and thus provides

important age constraint on the Mt. Simon and Wonewoc Formations (Hughes et al., 1997; Aswasereelert et al., 2008).

The Wonewoc Formation is dominated by mature quartz sandstones to orthoquartzites with minor carbonates and shales, representing deposition in offshore, inner shelf and shoreface environments (Runkle et al., 1998). Sedimentary structures and trace fossil assemblages are consistent with those of the Mt. Simon Sandstone; obolleid brachiopods and “*Cedaria*,” *Crepicephalus*, *Aphelaspis*, *Dunderbergia*, and *Elvinia* trilobite zones suggest this unit straddles the Dresbachian/Franconian boundary (Runkle et al., 1998).

At Blackberry Hill, Wisconsin, biostratigraphically useful fossils do not occur and the Eau Claire Formation is absent. Because it is not possible to ascertain which of these two Elk Mound sandstone units these new arthropods come from, or if the Wonewoc and Mt. Simon are superposed in outcrop, all described material is referred to the Elk Mound Group. Fossils occur in fine to medium grained clean quartz orthoquartzites immediately adjacent to a shallow channel (Figure 1E) and occur as positive impressions on bed soles with abundant polygonal mud cracks indicating subaerial exposure (see stratigraphic column, Figure 1E).

Lodi Member of St. Lawrence Formation

In western Wisconsin, the Lodi Member is part of the Furongian (Trempealeauan) St. Lawrence Formation, which underlies the Jordan Formation and overlies the Tunnel City Group which itself overlies the Elk Mound Group (Byers and Dott, 1995; Hughes and Hesselbo, 1997). Biostratigraphically, the St. Lawrence was

deposited during in the *Saukia* zone (*sensu* Raasch, 1951). The St. Lawrence is a thin (15–20 m), laterally extensive shallow marine unit, composed largely of a mixture of silty shale, very fine sandstone and dolomite (Byers and Dott, 1995; Hughes and Hesselbo, 1997). The St. Lawrence contains a number of well-preserved invertebrate fossils, including aglaspids and trilobites (Byers and Dott, 1995; Hughes and Hesselbo, 1997). In western Wisconsin and eastern Iowa, the Lodi Member consists of a burrowed, ripple marked, dolomitic siltstone to fine sandy dolomite with wavy shaley partings and local stromatolites (Anderson et al., 1979; Byers and Dott, 1995). Lithofacies present in the St. Lawrence indicate a shallow marine environment with episodically changing current directions and episodic storm deposits; this unit has been interpreted as the toe-set of a transgressive shoreface that migrated northward with sea level rise (Hughes and Hesselbo, 1997). The paleolatitude of the Lodi and the Potsdam Group (below) did not differ significantly from the Elk Mound; all were at tropical latitudes.

Potsdam Group

The Potsdam Group of Southwestern Quebec is a typical epicratonic cover that forms an extensive blanket of sandstone that unconformably overlies the crystalline Precambrian rocks of the Grenville structural province (Figure 1B). The local sedimentary depositional sequence begins with a siliciclastic-dominated succession. At the base is the feldspathic and conglomeratic Covey Hill Formation. Based on primary structures and bed thickness, its depositional environment is interpreted as a complex

interfingering of initially aeolian and braided fluvial facies (Hofmann, 1972) with gradually more shallow-marine influence.

The clean quartz sandstones of the Cairnside Formation disconformably overlie the Covey Hill Formation. This Formation records the first marine advance over the cratonic lowlands. It was deposited during a widespread eustatically-driven transgression. The Cairnside is fairly homogeneous throughout its exposure; it consists mainly of medium to coarse-grained, thick to medium-bedded mature quartz arenites. Sedimentary structures, trace fossils, and body fossils of the Cairnside Formation indicate a tide dominated, shallow subtidal to intertidal deposetting, possibly with shoreline sand bars (Salad Hersi and Lavoie, 2000). Prominent sedimentary structures include planar bedding, current ripples, adhesion ripples and polygonal desiccation cracks.

The most common types of fossils in the Cairnside are trace fossils such as *Arenicolites*, *Climactichnites*, *Cruziana*, *Diplichnites*, *Protichnites*, and *Skolithos*. Very rare phosphatic remains of lingulate brachiopods have also been reported (Clark, 1966). Despite the fact that the Potsdam of Quebec has been of paleontological interest since mid-19th century (e.g., Logan, 1851; Owen, 1852) only recently have body fossils been reported (Collette and Hagadorn, 2008; Lacelle et al., 2008). Potsdam arthropods reported herein are preserved in life position (ventrally), in convex hyporelief on bed soles, in fine- to medium-grained, sub- to well-rounded, clean quartz arenites and orthoquartzites.

Methods

Large fossil-bearing slabs were photographed, gridded and mapped, cast, and described in the field. Where possible, slabs were trimmed to sub-meter sized specimens in order to reposit them in museums. Camera lucida drawings of selected fossils were done with both a field-based lucida unit (Holbein), and with a Nikon binocular microscope fitted with a lucida attachment. In all camera lucida drawings, gray represents deep relief, and white represents high relief. Morphometric parameters were measured with digital calipers. For field specimens too large to collect, a reinforced latex mold of the original surface was produced, from which a subsequent plaster facsimile of the original surface was reproduced. The length of curving or otherwise convoluted trackways was measured with string that had 1 cm increments marked along its length. Specimens in this study are reposit in the collections of the Paleontological Research Institution, Ithaca, New York (PRI); the Pointe-du-Buisson Archaeological Park, Beauharnois, Quebec, Canada, (PDB); the Royal Ontario Museum, Ontario, Canada (ROM); and the University of Wisconsin Geology Museum (UWGM). Throughout this contribution, the nomenclature for arthropodan limb tagmosis outlined by Boxshall (2004) is followed.

Systematic Paleontology

SUBCLASS Phyllocarida PACKARD, 1879

ORDER Archaeostraca CLAUS, 1888

FAMILY unassigned

ARENOCARIS new genus

Type species.—*Arenocaris inflata* by monotypy

Diagnosis. —Valves ovate to subovate in outline, posterior margin convex.

Surface of carapace may have evenly spaced striations that parallel the carapace margin. Hinge line flat to very slightly convex; median dorsal plate absent. Narrow ventral margin present; extends from the anteriodorsal to posteriodorsal surfaces. Substantial ventrally reflected outgrowth of carapace (doublure) present. Abdominal somites increase slightly in length from anterior A1 to posterior A7.

Etymology.—*Arenatus*—covered with sand; *caris*—shrimp; refers to the unusual style of preservation in sand.

ARENOCARIS INFLATA new species

Figures 3A–G, 4A–G, 9A

Diagnosis.—As for genus.

Description.—Carapace. Length to depth ratio of carapace 1.66–4.46 ($n = 19$, $\bar{x} = 2.69$). Valve lengths (unbroken examples) are 28.6–36.2 mm, $\bar{x} = 32.6$ mm. Valve depths are 10.7–18.5 mm, with substantial variance due to the three-dimensionality of the fossils and the degree of taphonomic flattening; mean measured from complete carapaces (articulated valves) is 11.8 ($n = 10$), mean of flattened examples 18.11 ($n = 2$). Carapace valves ovate in outline when flattened; valve morphology varies in three-dimensionally preserved examples, which are ovate to subovate in outline. Carapace valves smooth; dorsal surface evenly convex in cross-section, becoming slightly less convex ventrally. Hinge line nearly flat to very slightly convex. Narrow thickened ventral margin present, carapace valves reflected into a true ventral doublure (Figures

4B, 5B). Ornamentation of the carapace valves may be present; consists of a series of very closely-spaced raised ridge-like features that parallel the posterior and postero-ventral carapace margins. Median dorsal plate absent, no evidence of anterior rostral plate known. No exterior carapace nodes present.

Thorax. No complete, intact example of the thoracic region known.

Abdomen. Abdomen composed of seven somites, gradually increasing in length posteriorly from somite A1 to pre-telson somite A7 (Figures 3E, 4E).

Abdominal somites are slightly compressed cylinders in cross-section, decreasing slightly in width toward the posterior of the abdomen. Surface of abdomen smooth; no evidence of ornamentation present on abdominal somites. Ratios of body segment lengths: A7:A6, 1.15–1.52 ($n = 3$, $\bar{x} = 1.32$); A6:A5, 1.21–1.25 ($n = 3$, $\bar{x} = 1.23$); A5:A4, 1.08–1.45 ($n = 3$, $\bar{x} = 1.3$); A4:A3, 1.13 ($n = 1$); and A3:A2, 1.03 ($n = 1$).

Pleopods present on somites A1 to A5, somites A6 and A7 apodous; pleopods insert ventromedially along the trunk, at the anterior margin of each limb-bearing somite.

Telson and furcal rami unknown.

Thoracic appendages. Incompletely known. Unknown number of paired thoracopods present; insert ventromedially along thorax, very closely spaced anterior-posteriorly (Figures 3D, 4D). At least two limb elements present: basal element small, roughly circular in outline, semi-circular in cross-section (length 1.8–2.55 mm); distal element long, relatively narrow, extending distally to near anterior carapace margin, no evidence of additional division in this element (length and width vary substantially and cannot be accurately measured due to preservation). Flattened, paddle- or oar-like elements often present toward the anterior of the ventral side of the carapace. Tightly

packed, imbricated structures (Figures 3C, 4C ‘th’) are occasionally present in the anterior of the carapace in the thoracic region.

Abdominal appendages. Five pairs of biramous pleopods present; pleopods insert ventromedially along abdomen (Figures 3A–D, 4A–D). Pleopods comprise three limb elements: a proximal uniramous limb element (protopodite) terminating distally in two rami; an endopodite located on the ventral side of the trunk that articulates with the distal end of the protopodite; and an exopodite located dorsolaterally, sharing the distal articulation with the protopodite. **Protopodite**—Protopodite short, rectangular to nearly round, average length to width ratio 1.86 (n = 11), length from 2.3 – 4.6 mm, width from 1.5 – 2.5 mm. Protopodites decrease in both length and width posteriorly, appears slightly flattened. Protopodites present on abdominal somites A1 to A5. In some examples, there appear to be well-developed ridges (Figure 3C, 4C ‘r’) extending longitudinally along the ventral surface of the protopodite. **Endopodite**—Inner abdominal limb ramus incompletely known. **Exopodite**—Outer abdominal limb ramus relatively large in comparison to other limb elements; often extends from nearly the ventral body axis to the inner carapace margin, foliaceous, decrease markedly in length and width posteriorly. Exopodites often U-shaped in cross-section, vary in length from ≤ 7.2 to ≤ 8.2 mm. Pattern of arcuate, raised, possibly imbricate features may be present. No evidence of setation on any thoracic or abdominal limbs.

Etymology.—*Inflata*—inflated, referring to the uncompressed nature of the fossils.

Holotype.— PRI 10130 (Figures 3A, 4A) a partial phyllocarid, consisting of abdomen, abdominal appendages, carapace valves, and a number of poorly preserved structures at the anterior end that probably represent thoracopods.

Other material examined.—PRI 10131–10142; UWGM 745, ten unnumbered UWGM specimens.

Occurrence.—Elk Mound Group, Furongian (Dresbachian to Franconian), Wisconsin; Lodi Member of the St. Lawrence Formation, Furongian (Trempealeuan), Wisconsin.

Discussion.—The Subclass Phyllocarida is both a long-lived and morphologically varied group of malacostracan crustaceans that has been well documented throughout much of the Phanerozoic, and includes 32 living representatives (Haney and Martin, 2000). The earliest phyllocarids previously known, the caryocarids, are known from the Early Ordovician, with as many as four species first appearing in the Tremadocian (see summary in Vannier et al., 2003). *Arenocaris inflata* is the first pre-Ordovician phyllocarid, and demonstrates that malacostracans existed in the Cambrian (Dahl, 1984; Walossek, 1999). Superficially similar bivalved arthropods of the Burgess Shale and Chengjiang Biota, such as *Canadaspis*, *Kunmingella*, *Odaraia*, *Perspica*, *Plenocaris*, and *Waptia*, are excluded from the Crustacea, and therefore the Phyllocarida, because of major morphological disparities in either body segment number, limb morphology, or both (Dahl, 1984; Hou and Bergström, 1997; Walossek, 1999; Hou et al., 2004). The definition of Phyllocarida emended from Rolfe (1981) is used here: Malacostraca with large carapace of two valves, with or without hinge line along the dorsal margin, connected by adductor

muscle, with or without movable articulated rostral plate. Thorax composed of eight short somites; abdomen of seven somites and telson, telson bearing unsegmented, articulated furcal rami.

In all but a handful of phyllocarid taxa, limbs are virtually unknown, hampering accurate diagnosis [e.g. *Nahecaris stuerzi* from the Devonian Hunsrück Slate (Bergström et al., 1987); *Cinerocaris magnifica* from the Silurian Herefordshire Lagerstätte (Briggs et al. 2003)]. Thus, phyllocarids from the Blackberry Hill Lagerstätte are strikingly unusual not only because they are preserved in three dimensions, but because limbs are also present. In nearly all examples, it is the pleopods that are best preserved. Thoracopods were much more closely spaced, and likely much less robust than were the pleopods, and thus are preserved infrequently and poorly. In one example (Figures 3D, 4D arrowed ‘th’), at least three pairs of anterior thoracopods are preserved. Segmentation of these limbs cannot be characterized in great detail, but structure is certainly apparent. Proximal, ventromedially located thoracopod elements (‘pe’) are evident in this specimen. In some examples, tightly packed, imbricated structures (Figures 3C, 4C ‘?th’) interpreted as thoracopods are present in the thoracic area of some examples. Because these appendages are imbricated and in their original position, the structure of the protopodites, exopodites, endopodites, and other limb elements are unknown. Flattened, paddle- or oar-like elements are occasionally present toward the anterior of the ventral side of the carapace (Figures 3A, 4A). These are interpreted as poorly preserved thoracopods or thoracopod elements.

The pleopods are preserved with much better clarity, and so can be interpreted with a good degree of accuracy. It should be noted, however, that these animals were likely attempting either to burrow or to escape just prior to death, and therefore it is possible that the limbs have been elongated or otherwise distorted by back-and-forth and/or up-and-down motion of the limbs during this effort. Similarly, preservation varies widely from specimen to specimen depending upon how much sand loading occurred during casting of the fossils, whether mud cracks are present, the local grain size, and the thickness of underlying mud layer.

In nearly all cases some of the abdominal limb elements are distorted, broken, missing, or obscured. However, a survey of all specimens possessing limb information reveals that the pleopods of *Arenocaris inflata* n. sp. appear to be composed of the typical crustacean limb tagmata: protopodite, endopodite, and exopodite (Figures 3A–D, 4A–D), although the full extent of some of these individual elements remains unclear.

The most proximal abdominal limb element in *Arenocaris inflata* n. sp., the protopodite, appears to be undivided (Figures 3A, G; 4A, G arrowed ‘p’), however, very infrequently, segmentation does appear to be present. In these rare instances, it appears possible that the protopodite may be divided into a proximal element, and a distal element (Figure 3A, 4A arrowed ‘?pe,’ and ‘?de’). The function of the longitudinal ridges that are infrequently preserved (Figure 3C, 4C ‘r’) is uncertain; they may have served to reinforce the protopodite while burrowing through mud or resistant quartz sand.

At the distal end of the protopodite, two rami are present: a broad, flattened, foliaceous outer ramus, and an incompletely known inner ramus. The foliaceous outer ramus, or exopodite, is quite large, often draping over the dorsal side of the protopodite and extending from the body center line to the inside edge of the carapace (Figures 3A, B; 4A, B ‘ex’). The exopodites appear U-shaped in cross-section and partially folded over themselves, often occluding details of the underlying limbs. In the holotype (PRI 10130), the exopodite of the first pleopod has a distinctive arcuate pattern of raised, possibly imbricate features. The purpose of this feature is unknown, and has not been previously reported in phyllocarids.

The inner rami, or endopodites (Figure 4B, 4G ‘en’), are not well known. Their presence can be inferred from limb-like structures that extend away from the presumed articulation with the protopodite, which is often either broken off or obscured by the exopodite. Limbs of the cephalic area are unknown.

Segmentation in the abdomen is well preserved in several specimens. Like the majority of Archaeostraca, as well as in the living Leptostraca, the abdominal somites in *Arenocaris inflata* n. sp. gradually increase in length toward the posterior of the animal. Unfortunately, with preservation in fine to medium sand, any ornamentation that may have been present on the abdominal segments is not preserved.

The carapace valves of *Arenocaris inflata* n. sp. are ovate to subovate in outline with a slightly concave dorsal margin. Overall this valve shape is very reminiscent of modern leptostracan carapace shape. However, in *Arenocaris inflata* n. sp., the valves are quite thick [0.9 – 1.27 mm thick, \bar{x} = 1.11 mm (Figures 3B–D, 4B–D)] and have a well-developed doublure [3.0 – 4.3 mm, \bar{x} = 3.5 mm (n = 3) (Figure 3B, 4B ‘do’)].

Evidence from an internal mold of a carapace indicates that the carapace valves may have been ornamented with a series of raised, concentric, closely spaced striations that parallel the ventral and posteroventral carapace valve margins; the unusual internal geometry of these field specimens inhibited photography of the ornamentation. A similar style of carapace ornamentation has been documented in the Silurian archaeostracan genus *Ceratiocaris*, where these structures may have served to stiffen a relatively thin and flimsy carapace. Because the carapace valves of *Arenocaris inflata* n. sp. are thick, possess a robust doublure, and have a thickened margin, it would seem additional stiffening would not be necessary. Such a carapace might, however, serve as protection from predators.

The Lodi Member of the St. Lawrence Formation contains comparable, but stratigraphically younger, phyllocarids (Figure 3F, 4F). Phyllocarid carapaces from the Lodi Member are substantially flattened; however, they do retain a degree of three-dimensionality even after compression, indicating a substantial thickness. These carapace valves are considered to be cf. *Arenocaris inflata* based on overall carapace shape and substantial thickness of the valves. A pair of nearly articulated valves (Figures 3F and 4F) illustrates the similarity to Elk Mound Group phyllocarids; the valves are both slightly inflated, and sand fills the interstitial space. A well-preserved, thin ventral margin is present along both outer carapace valve margins. No nodes of the carapace are present in any of the Lodi Member material.

In addition to the three-dimensionally preserved phyllocarids in the Elk Mound, relatively flat phyllocarid impressions also occur. In these examples, details of the limbs are much less resolved, and the animals often appear partially disarticulated.

Figures 3E and 4E show a compressed phyllocarid that comprises all seven abdominal somites, both carapace valves, and an enigmatic circular to ovoid impression in the area immediately anterior of the carapace valves that could represent a rostrum. However, in this specimen, the ratios of lengths of the abdominal somites to each other are distorted when compared to the three-dimensional specimens, possibly due to telescoping of abdominal somites after death. In another compressed specimen (Figures 3G, 4G), the posteriormost two pairs of abdominal limbs appear to be in place, but anterior to these, the limbs appear to be partially disarticulated. These flattened, apparently disarticulated isolated individuals are rare, and may represent exuviae.

It is interesting that not a single definitive example of a telson or furca is preserved, either isolated or in connection with a phyllocarid. A small part of a possible telson may be preserved in connection with the posterior of somite A7 in the uppermost of the three phyllocarids present in Figure 3B. Unfortunately, this structure was broken during excavation or transportation of the slab. Because the telsons in many phyllocarids are blade- or leaf-like, and they are located at the distal end of the body, it is possible that the telson did not impress deeply enough into the substrate to form a mold.

The alignment of the arthropods in Figure 3B and 4B is similar to that shown by Hou et al. (2008), in which aligned *Waptia*-like arthropods from the Chengjiang Lagerstätte were described. Chains of as many as 20 individuals of this Cambrian arthropod have been recovered; these have been interpreted as a collective strategy for migration or defense (Hou et al., 2008). The three aligned specimens of *A. inflata* n. sp. are substantially larger than are the Chengjiang examples (2.27 cm length in the

Chengjiang examples, 4.5 cm in a nearly complete example of *A. inflata*), indicating a greater mass. Considering the paleoenvironment in which they were found, and their greater mass, a migration strategy for these aligned arthropods is not supported. It is possible that these three aligned specimens were mating, but it is also possible that they were simply following each other in an attempt to return to deeper water. Indeed, they are preserved at the edge of a channel levee.

Nearly half of the Elk Mound phyllocarid remains recovered from the main fossil-bearing bed sole (Figure 2A) are oriented in one of two main directions, with one node trending toward 310°, and one trending toward 190°. The phyllocarids are preserved in the overbank portion of a shallow channel, and are distributed from the levee bank to more distal, topographically lower areas (i.e., toward the bottom of the slab in Figure 2A). The bimodal distribution of phyllocarid body fossil orientations suggest that the phyllocarids were attempting to either: return to the channel (310° mode), or move toward the deeper portions of the flooded banks (190° mode).

CLASS Euthycarcinoidea GALL AND GRAUVOGEL 1964

FAMILY uncertain

MOSINEIA new genus

Type species.—*Mosineia macnaughtoni* by monotypy.

Diagnosis. —Large, prominent preabdomen. At least seven thoracic segments. Postabdomen apodous, composed of six segments and telson. First preabdominal somite greatly reduced, subsequent somites approximately same length, but decreasing

in width posteriorly. Telson blade-like, no rami; approximately three times the length of the posteriormost abdominal segment.

Etymology.—Named after Mosinee, Wisconsin, the place where these arthropod fossils were discovered.

MOSINEIA MACNAUGHTONI new species

Figure 5A–5D, 9B

Diagnosis.—As for genus.

Description.—Body with distinct tagmosis; divided into limb-bearing preabdomen, and apodous postabdomen terminating in a telson. Cephalic region unknown.

Preabdomen. Details of the dorsal surface unclear, appears to consist of a large plate or series of plates that are convex in cross-section; outline of dorsal margins in ventral view roughly oval; dorsal surface narrower at anterior and posterior margins. Imbricate features may be present in carapace region (Figure 5A, B arrowed ‘i’). Ventral preabdominal segmentation has not been directly observed, but its presence is inferred by the presence of limbs. Preabdomen of at least seven limb-bearing sternites; appears to reach its maximum width at the third or fourth sternite from the anterior margin of the preserved portion of the preabdomen.

Postabdomen. Composed of six apodous somites, terminating in telson. First postabdominal segment (A1) greatly reduced anteroposteriorly, approximately one-third the length of subsequent somites (Figure 5A–D labeled ‘A1’). Postabdominal somites A2 – A6 of similar length, width decreases slightly posteriorly with each

somite (Figure 5B, D). No postabdominal ornamentation known. Telson elongate, blade-like, unornamented; broad at junction with postebdom, tapering to a rounded terminus. Length of telson corresponds to at least three abdominal somites (Figure 5B arrowed 't').

Thoracic limbs. At least seven pairs of apparently uniramous limbs present. Limbs insert very closely along ventromedial surface of thoracic trunk, with proximal limb elements of limb pairs nearly touching medially. Occasional raised ramifications present proximally [Figure 5D, arrowed 'pe' (proximal element)]. Limbs flattened, appear paddle-like; limb segmentation not well-defined, possibly three elements preserved.

Etymology.—Named in honor of the discoverer of the main Wisconsin arthropod-bearing surface, Rob MacNaughton.

Holotype.—PRI 10144 (Figure 5A, B), a ventrally-preserved partial specimen, consisting of five postabdominal somites with articulated telson, and a preabdominal area with an unknown number of somites.

Other material examined.—PRI 10141, a plaster cast of a field specimen, PRI 10145.

Occurrence.—Elk Mound Group, Furongian (Dresbachian to Franconian), Mosinee, Wisconsin.

Discussion.—Details of the dorsal surface of *M. macnaughtoni* n. sp. are unclear. The general outline suggests an oval shape in ventral view (Figure 5B), and a series of linear, imbricate features suggest that the dorsal surface may have been composed of a series of dorsal tergites. Details of the cephalic area are unknown.

Limb segmentation is poorly understood in *M. macnaughtoni* n. sp., with very few instances where individual limb elements can be observed. In Figures 5C and D, very subtle changes in relief along limbs indicates that at least two limb elements (possibly as many as three) may be present: a proximal element (arrowed 'pe'), and a more distal, straight, broad, and possibly flattened element. It is possible that these flattened limbs could have been useful in swimming, although this flattening could simply be due to taphonomic processes such as post-burial compaction.

The tagmatization between the limb-bearing preabdomen and apodous postabdomen is manifested in both known specimens as an anteroposteriorly reduced somite (Figures 5A–D labeled A1), which is attributed to the postabdomen based on its lack of appendages. Subsequent postabdominal somites are approximately the same length, but decrease slightly in width along the trunk (PRI 10144: A1 – 1.45 mm long, A2 – A6 – 3.58 to 4.92 mm long; width from A2 to A6 – 13.31 to 9.33 mm; PRI 10145: A1 – 2.29 mm long, A2 – A6 – 6.25 to 6.8 mm long; as this specimen is broken along its left side, width data is incomplete. One well-preserved somite (Figure 5B labeled 'A6') shows a subtle narrow lip on the anterior ventral surface. This may represent the articulation between abdominal segments. A large mud crack is present along the entire right side of this specimen. Thus, it is likely that the telson in this specimen is incompletely preserved, and may be substantially longer. No rami appear to be present.

These large arthropods (9.04 to ≥ 10 cm in length) might represent the producer of a number of *Diplichnites*- and/or *Protichnites*-like trace fossils from the Elk Mound Group of Wisconsin. Well-preserved in-phase *Diplichnites* and *Protichnites* trackways generally have 6 – 9 pairs of ped impressions (Hoxie, 2005), corresponding with the

number of limbs thus far observed in *M. macnaughtoni* n. sp. Many of these trackways also have a distinct medial furrow, and their overall width (Hagadorn and Seilacher, 2009) is consistent with that of *M. macnaughtoni* n. sp. (5.1 1–6.7 cm wide). In Elk Mound *Diplichnites* and *Protichnites*, the most widely spaced ped impressions are at the anterior end of each set within the trackway, and a gradual decrease in the width of the trackways occurs with each subsequent posterior ped impression (Hoxie, 2005; Hagadorn and Seilacher, 2009); the more robust anterior limbs of *M. macnaughtoni* might be expected to produce similar trackway sets.

Because only three specimens of *Mosineia macnaughtoni* n. sp. are known, and because these are incompletely preserved, it is possible that this species may represent an occurrence of the new family described below. These new arthropods share a number of morphological characters with the Euthycarcinoidea, including: possible dorsal-ventral segment mismatch, a six segmented postabdomen (in Cambrian species), and a blade-like telson lacking rami. However, because the appendages of *M. macnaughtoni* insert much more closely to the ventral midline than do other euthycarcinoid appendages, and because euthycarcinoid limbs are composed of many more (up to 24) comparatively much smaller box-shaped limb elements, *Mosineia macnaughtoni* n. sp. is likely a stem-group member of the class Euthycarcinoidea.

FAMILY Mictomeridae new family

MICTOMERUS new genus

Type species.—*Mictomerus melochevillensis* by monotypy.

Diagnosis. —Large dorsal shield composed of overlapping, dorsal tergites.

Eleven preabdominal sternites, each bearing a pair of homopodous limbs. Limbs insert very close to the ventromedial axis of body, producing a ventromedial groove.

Postabdomen apodous, composed of at least five somites of similar length; abdominal somites decrease slightly in width posteriorly. Telson unknown.

Etymology.—From miktous (Greek) meaning mixed or blended; and meros (Greek) meaning parts. Refers to the strange mixture of morphological parts, which seem drawn from both euthycarcinoids and aglaspidids.

MICTOMERUS MELOCHEVILLENSIS new species

Figures 5E–F, 6A–G, 7A–G, 8A–F, 9C.

Diagnosis.—As for genus.

Description.—Cephalic area.—Poorly known. Anterior of cephalic area convex, equal to approximately one-third overall width; rapidly becoming concave before again becoming convex. A laterally elongate oval structure is present in the anteriormost cephalic area (Figures 6D, 7D arrowed ‘la’). This structure has a narrow medial invagination present in the posterior edge of this structure that is aligned with the ventromedial axis of the trunk; margins of slot opening smoothly convex, apex of slot acutely pointed. This slot is approximately one-half of the anterior-posterior length of

the structure. A pair of laterally placed, spherical structures (Figures 6B, F; 7B, F labeled 'e') are immediately posterior to the slotted oval structure.

Thorax. Large preabdominal tagma (referred to as thorax hereafter) consisting of five to six overlapping dorsal tergites (Figures 6A, G; 7A, G; 8E, F arrowed 'te'). Greatest width occurs in first half of thoracic area. Posterolateral margins of dorsal tergites vary substantially from rounded (Figure 6A, 7A arrowed 'te'), to distinctly truncated at the juncture of the ventral and posterior margins (Figures 6G, 7G, 8E–F arrowed 'te'). Posterior margin of last tergite may be rounded (Figure 7E 'pm'). The extent of posterior projection of the dorsal tergites varies from nearly no overlap with the abdomen (e.g. Figure 7A) to perhaps the midpoint or end of abdominal somite one (Figure 7E, 8F). Dorsal surface of tergites unknown. Thoracic segmentation has not been directly observed; its presence is defined by limbs. Thorax of up to eleven limb-bearing segments.

Abdomen. Abdomen composed of at least five apodous somites of similar length, decreasing very slightly in width posteriorly (Figure 5E–F; 7A–B, E–F). Lateral margins of abdominal somites straight, posterolateral margins sharply truncated. Abdominal ornamentation absent; telson unknown.

Thoracic limbs. Up to eleven pairs of homopodous thoracic limbs present; limbs composed of three to five elements. The proximal limb element is short, wide, and usually has more relief than the distal limb elements. Second and third elements slightly longer than the proximal element, straight, tubular; approximately the same length. Occasionally, two additional limb elements of similar size and shape as the immediately preceding element may be present (Figure 6D, 7D numbered). Limb pairs

insert ventromedially along trunk, decrease in size posteriorly; limbs evenly spaced anteroposteriorly along the trunk. A narrow recess is developed between the proximal limb element of each limb pair; together, these recesses form a linear, anteroposterior recess running the length of the thorax (Figure 5E–F, 6A, 7A).

Etymology.—Named after Melocheville, Quebec, Canada, where the holotype was discovered. Entire binomial name meaning: (animal with) a strange mixture of parts coming from Melocheville.

Holotype.—ROM 59386, a ventrally-preserved, nearly complete animal consisting of thorax, thoracic limbs, and abdomen.

Other material examined.—ROM 59387, a single incomplete individual; A field slab consisting of a bed sole with 30 ventrally-preserved arthropods.

Occurrence.—Potsdam Group, Furongian, Melocheville, Quebec, Canada.

Discussion.—Studies of fossilization potential in a modern cold water intertidal environment (Friday Harbor, WA) indicates that as much as 29% of the total fauna might be expected to fossilize in low energy sand-dominated environments (Schopf, 1978). However, articulated body fossils are virtually unknown from sand-flats (Hagadorn and Belt, 2008). Given the rarity of preservation in such lithofacies, it is plausible that these arthropods represent an extinct stem lineage that has never been seen before.

Indeed, *M. melochevillensis* n. sp. has a peculiar collection of characters: dorsal-ventral segmental mismatch; uniramous, homopodous limbs with a pronounced proximal ramification; and a linear ventromedial groove. This taxon may also possess a labrum with a rearward-oriented opening [Figures 6B, D, F; and 7B, D, F (arrowed

‘la’)]. The very closely-spaced limbs and the linear ventromedial groove (Figure 5E–F), suggest that *Mictomerus melochevillensis* n. sp. has a gnathobasic, or coxa style of food transport and processing. The first pair of limbs is immediately posterior to the labrum, and appears to make contact with it (Figures 7D, F); in most specimens, a distinctly developed proximal ramification is present. No coxal ‘teeth’ have been observed.

The anterior, laterally placed hemispherical structures (Figures 6B, F; 7B, F) are interpreted as eyes. Their placement is coincident with the posterior terminus of a tergal plate (Figures 6B, 7B), perhaps the only tergal plate of the cephalic region. It is not known whether an additional, smaller tergal plate was located anterior to the first large tergite, but an impression anterior to the labrum in Figure 7D suggests this adjacency. There is no evidence to suggest that the eyes were stalked.

When limb segmentation is evident, the majority of specimens indicate three limb elements (Figures 7A, C; 8C, D). However, in one example (Figure 7D) it appears that five limb elements may be present. It is possible that additional limb elements were present in these arthropods, but are not preserved. In the reconstruction of *M. melochevillensis* n. sp. (Figure 9C), five limb elements are included. All of the limbs appear homopodous and decrease slightly in size toward the posterior of the animal, and appear fairly robust. The limbs do not appear to be flattened as in *Mosineia macnaughtoni* n. sp.. Eleven pairs of limbs are present in the best preserved example of *M. melochevillensis* n. sp. (Figure 6A, 7A), thus it is probable that it had eleven pairs of walking limbs. In one example (Figure 5E, F) an appendage is present in the anterior right side of the thorax that appears to articulate forward and have a substantial number

of elements. However, it is likely that this ‘appendage’ is in fact two appendages, where the anterior appendage is overlain by the immediately posterior one.

On one large bed sole, 28 well-preserved specimens are preserved along with their *Cruziana*-like trace fossils. A rose diagram of orientations of the arthropods (Figure 2B1) shows three main nodes. One node is oriented toward 75°, one toward 190°, and the third toward 310°. Sedimentary structures and the lithology of this slab suggest an overbank depositional environment similar to the environment of deposition of the phyllocarid-bearing bed sole from Wisconsin. Because this slab was collected from float, however, it is not possible to determine where the channel edges were located. Mud cracks present on the slab (Figure 2B1) cross-cut tracks and body fossils, and are polygonal with T-shaped intersections and upturned edges. Together, these features indicate subaerial desiccation of this surface after production of the traces and burial of the arthropods. Presence of first, second, and third order cracks requires the presence of a thick mud horizon, and either protracted or multiple episode(s) of subaerial exposure. Cracks on the left side of this slab are deeper than those on the right, indicating that this part of the bed surface must have been bathymetrically deeper than the right side of the slab. The 190° trending node shown on the rose diagram may indicate that arthropods were preferentially moving toward this deeper area of the slab, possibly seeking refuge in the only standing water still available.

Implications: Paleobiology, Paleoecology and “Euthycarcinoids”

A variety of arthropod trackways are preserved in the Potsdam Group, including *Cruziana*, *Diplichnites*, and *Protichnites* in intertidal facies (Bjerstedt and Erickson, 1989; Hagadorn and Belt, 2008), and *Diplichnites*-like forms and *Protichnites* in aeolian facies (MacNaughton et al., 2002) and are notable because they are the earliest evidence of animals on land. *Diplichnites* and *Protichnites* trackways may have been made by a homopodous arthropod that had a telson, such as a euthycarcinoid (MacNaughton et al., 2002). The new euthycarcinoids described herein represent a possible producer of protichnitid and diplichnitid trace fossils from the Elm Mound and Potsdam Groups.

Mictomerus melochevillensis n. sp. has all the morphological characteristics required to produce these traces; it has eleven pairs of limbs (some of which might not have been used for ambulation), a body having a long, narrow, postabdomen (and likely a telson as well), and homopodous limbs. MacNaughton et al. (2002) noted the robust nature of the appendage marks, suggesting a substantial body mass. However, many euthycarcinoids have limbs composed of a large number of thin, identical, box-like elements, often with feather-like setae present (Schram and Rolfe, 1982; Anderson and Trewin, 2003). These feather-like structures have been interpreted as adaptations for swimming (Schram and Rolfe, 1982; Anderson and Trewin, 2003), and could probably not support a large, heavy animal like *M. melochevillensis* out of the water. However, limb elements of another Cambrian euthycarcinoid, *Apankura machu*, are much more robust, and could possibly have supported its body weight subaerially (vaccari et al., 2004).

Aeolian arthropod trackways from the Potsdam of Ontario and New York show no evidence of body impressions other than intermittent drag marks interpreted as having been made by a telson (MacNaughton et al., 2002; Hagadorn, 2008). Sediment push-up mounds located posterior to ped impressions preclude an undertrack origin for these trackways, thus, the limbs of the tracemakers must have been both robust enough and long enough to have held these fairly large arthropods off the surface as they were climbing dune faces. The limbs of both *M. macnaughtoni* n. sp. and *M. melochevillensis* n. sp. appear to have been robust enough to have supported these arthropods for brief subaerial forays.

Mictomerus melochevillensis n. sp. possess multiple characters that allow its assignment to the Euthycarcinoidea. The presence of pre- and postabdomen tagmata, eleven pairs of homopodous appendages, dorsal tergites, and an anterioventral labrum are known to be present in a number of euthycarcinoid species. The euthycarcinoid family Kottixerxidae has five dorsal tergites, and it appears that the ‘carapace’ of *M. melochevillensis* n. sp. is also composed of a series of overlapping dorsal plates. Indeed, the major difference between *Mictomerus melochevillensis* n. sp. and all other known euthycarcinoids lies in the arrangement and makeup of the limbs and limb elements. In all other well-known euthycarcinoids, the many-segmented limbs insert along the anterior lateral margin of the pre-abdominal somites; and, although each limb element gradually increases in size toward the insertion point, there is no proximal ramification present on each limb in euthycarcinoids (Schram and Rolfe, 1982; Anderson and Trewin, 2003). *Apankura machu* appears to have more robust appendages than other post-Cambrian occurrences, but the morphology of the limb

insertion points is unclear in the only known example of this taxon. In *M. melochevillensis* n. sp., there are probably not many more than five limb elements preserved, a distinct proximal ramification is present in each limb, and the limbs insert much closer to the ventromedial axis of the trunk. These differences in limb morphology indicate that *M. melochevillensis* may be a stem-group euthycarcinoid, and possibly lies close to the branching point with crustaceans or a myriapod–hexapod assemblage.

The limbs of *M. melochevillensis* n. sp., however, are much more robust than all other known euthycarcinoid limbs. Its appendages are not well-suited for swimming because they appear to lack exopodites, because they are uniramous, and because they are homopodous. Together these features suggest that the animal walked along the bottom when ambulating subaqueously. Its robust appendages might have also facilitated lifting of its body off the substrate without the assistance of subaqueous buoyancy. *Mictomerus melochevillensis* n. sp. occurs in the Potsdam Group in rocks with abundant evidence of desiccation indicating that it inhabited environments that were subject to intermittent subaerial exposure. Given its morphology, size and location, *Mictomerus melochevillensis* n. sp. seems a likely candidate producer of subaerial trackways in the Potsdam Group.

Intertidal environments in the Potsdam Group may have been intermittently or persistently inundated with sufficient rainwater or fluvial derived runoff to yield brackish conditions. Channels associated with *A. inflata* and *M. macnaughtoni* may be fluvial or tidal in origin. Given the rapid evolution of euryhaline and freshwater tolerance among other marine arthropods such as eurypterids (Kues and Kietzke, 1981),

it is possible that Elk Mound and Potsdam taxa also survived periodic hyposaline conditions.

Conclusions

Arenocaris inflata n. sp. is the earliest known phyllocarid, pushing back the first occurrence of the Subclass Phyllocarida by 13 to 18 million years, to the Early-Mid Furongian. These phyllocarids are quite similar to modern leptostracan forms in the shape of the carapace and generalized abdominal morphology; however, they differ in their larger size, flap-like pleopod exopodites, and substantially thickened carapace valves with a well-developed doublure. *Mosineia macnaughtoni* n. sp., is a new type of large, unusual arthropod with possible ties to the Euthycarcinoidea, and may have been able to produce *Protichnites* and *Diplichnites*. *Mictomerus melochevillensis* n. sp. is another enigmatic large candidate producer of such trackways.

Coarse-grained siliciclastic strata are not thought of as conducive to preservation of soft-bodied or lightly mineralized animals, except in the Ediacaran. New fossils described here are a notable exception. Because they are preserved in a very narrowly defined environment (overbank of a shallow channel) characterized by the presence of large-scale desiccation features, they provide a new search image for identifying similar exceptional fossil deposits in the abundant epicratonic sheet sandstones of the early Paleozoic. Such deposits also have the potential to fill in gaps in our understanding of evolution in an environment that was likely important in early terrestrialization of animals.

Figure 1. Geological context of Elk Mound, St. Lawrence, and Potsdam exposures. A – Laurentia in the Late Cambrian (Furongian) with the locations of field sites starred along the shoreline. B – Outcrop map of the Potsdam Group in the New York/southern Quebec area, star represents field site, generalized stratigraphic column on far right. C – Geological map of Wisconsin, showing the distribution of Cambrian strata and location of field sites (stars). D – Generalized stratigraphic column of Cambrian strata of Wisconsin showing arrangement and approximate unit ages. Acronyms: SL – St. Lawrence Formation; TCG – Tunnel City Group; WSS – Wonewoc Sandstone; EC – Eau Claire Formation; MSS – Mount Simon Sandstone. E – Portion of the stratigraphic section of the quarry that the Elk Mound arthropods occur in [modified from detailed column in Hoxie (2005)]. Note the prominent channel also illustrated in Fig. 2A, and co-occurrence with both *Cruziana* and *Rusophycus*.

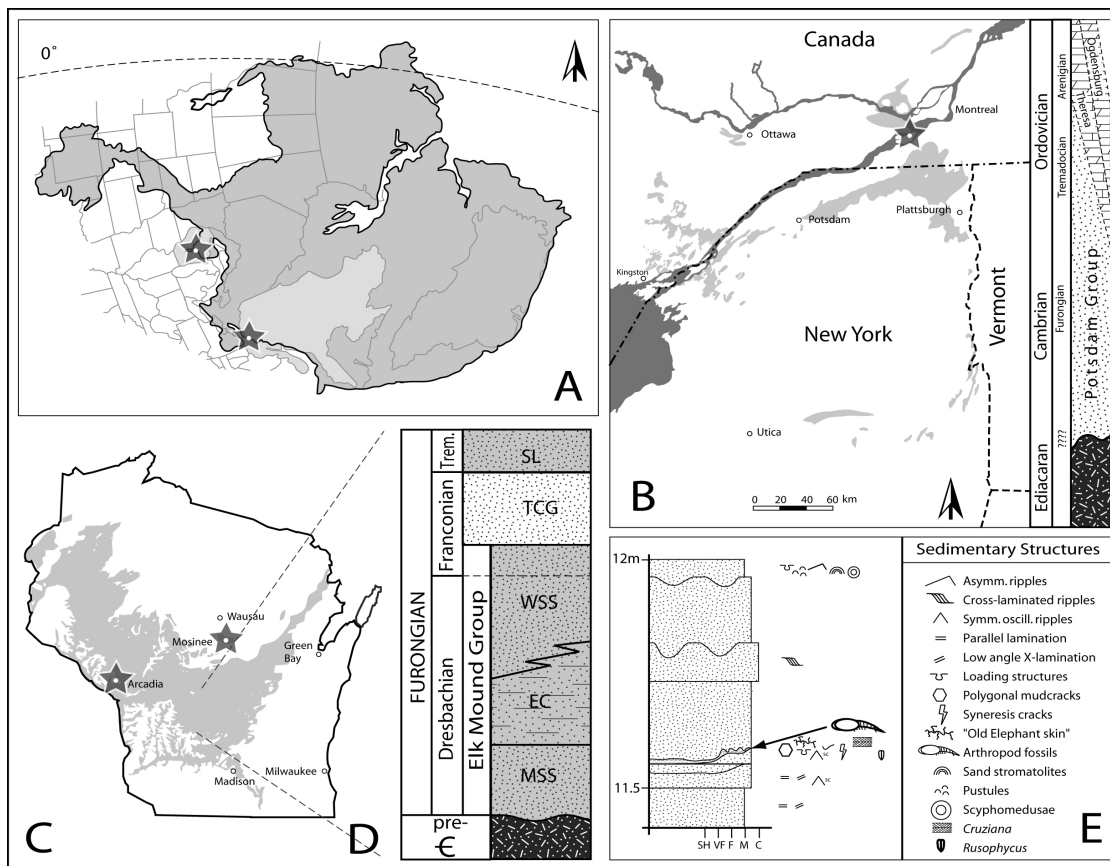


Figure 2. Arthropod-bearing bed soles from Wisconsin and Quebec. A1 – Gridded map of arthropod-bearing sole from the Elk Mound Group (PRI station 3421) showing distribution and orientation of arthropod body and trace fossils, note the prominent channel at top. Inset rose diagram shows the orientation of arthropod body fossils relative to the orientation of the slab in the map. Note two prominent directions of alignment, both away from the channel, and toward it (see text for discussion). A2 – photograph of one of the two blocks comprising the upper half of the grid map in Figure A1. Slab broke in half during transport from the field. Channel direction is toward the top in this photograph. B1 – Map of arthropod-bearing sole from the Potsdam Group (PRI station 3849), showing the distribution of fossils. Numbers indicate individual arthropod fossils referred in subsequent Figures. Note the thickest mudcracks are toward the lower left, and that arthropod trackways leading up to body fossils mediate the formation of mudcracks. Inset rose diagram shows the orientation of arthropods relative to the orientation of the slab in the map. Note the prominent node toward 310°, and one trending toward 190° (discussed in text). B2 – photograph of the slab shown in grid map B1. Scale bars = 1 m.

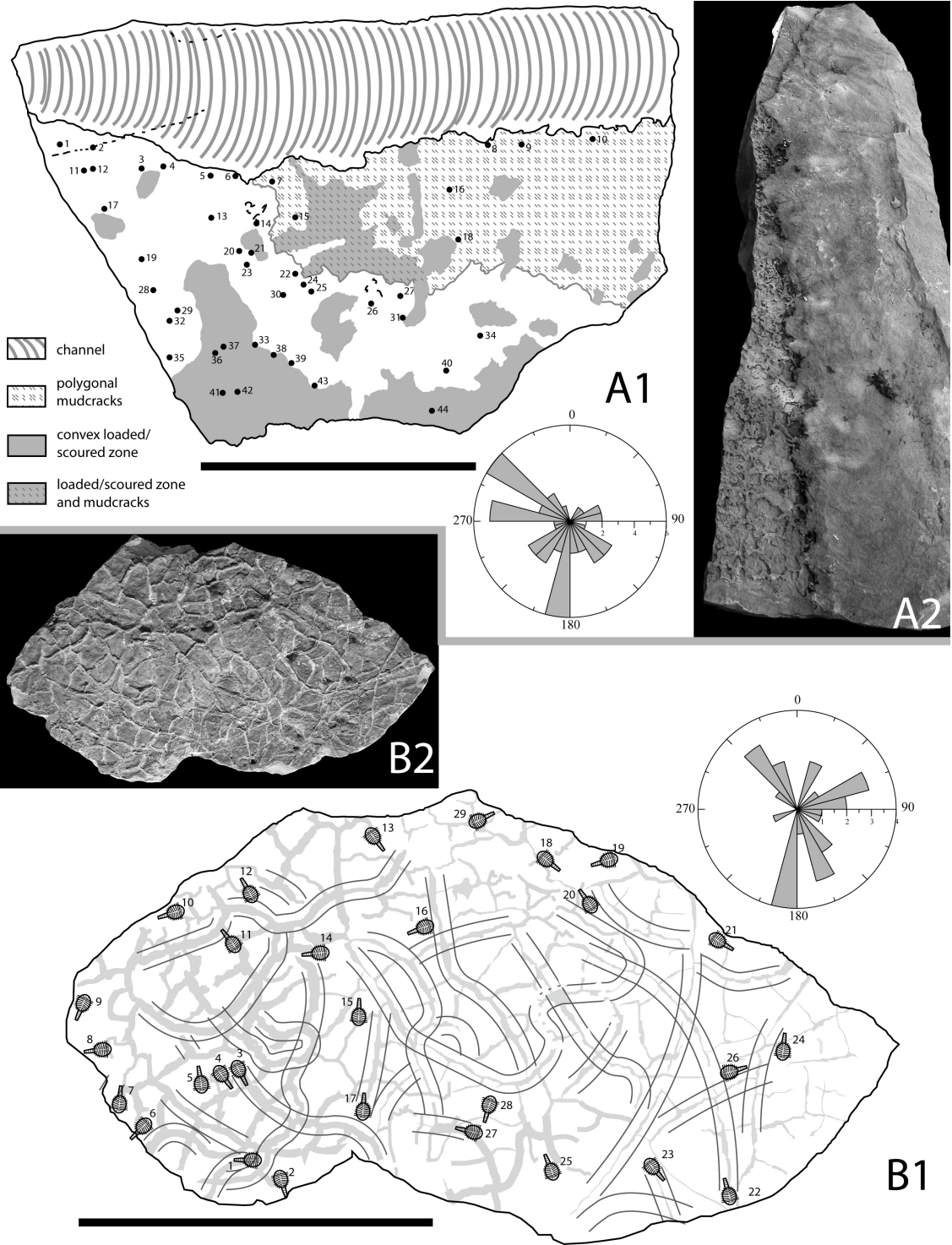


Figure 3. *Arenocaris inflata* n. gen., n. sp. from the Elk Mound Group. A – PRI 10130 (holotype), a nearly complete phyllocarid, note prominent limb bases (arrowheads). B – PRI 10131a–c, three phyllocarids (a at top, c at bottom); two partial, and one complete. The three-dimensional style of preservation is evident in this specimen. Note the thick carapace valves in the center specimen, as well as a portion of the doublure preserved on the right side (arrowhead). C – PRI 10131d, incomplete phyllocarid trunk showing limb morphology. D – PRI 10132a, incomplete phyllocarid abdomen and part of thorax illustrating abdominal, as well as thoracic limbs. E – PRI 10142, plaster cast of a nearly complete phyllocarid, an example of a more flattened style of preservation. F – cf. *Arenocaris inflata* carapace valves, UWGM 745, a pair of flattened phyllocarid carapace valves showing the thin ventral carapace margin and overall valve shape when flattened. G – field photograph of a flattened phyllocarid, but limbs and abdominal details are still visible. All scale bars = 1 cm.

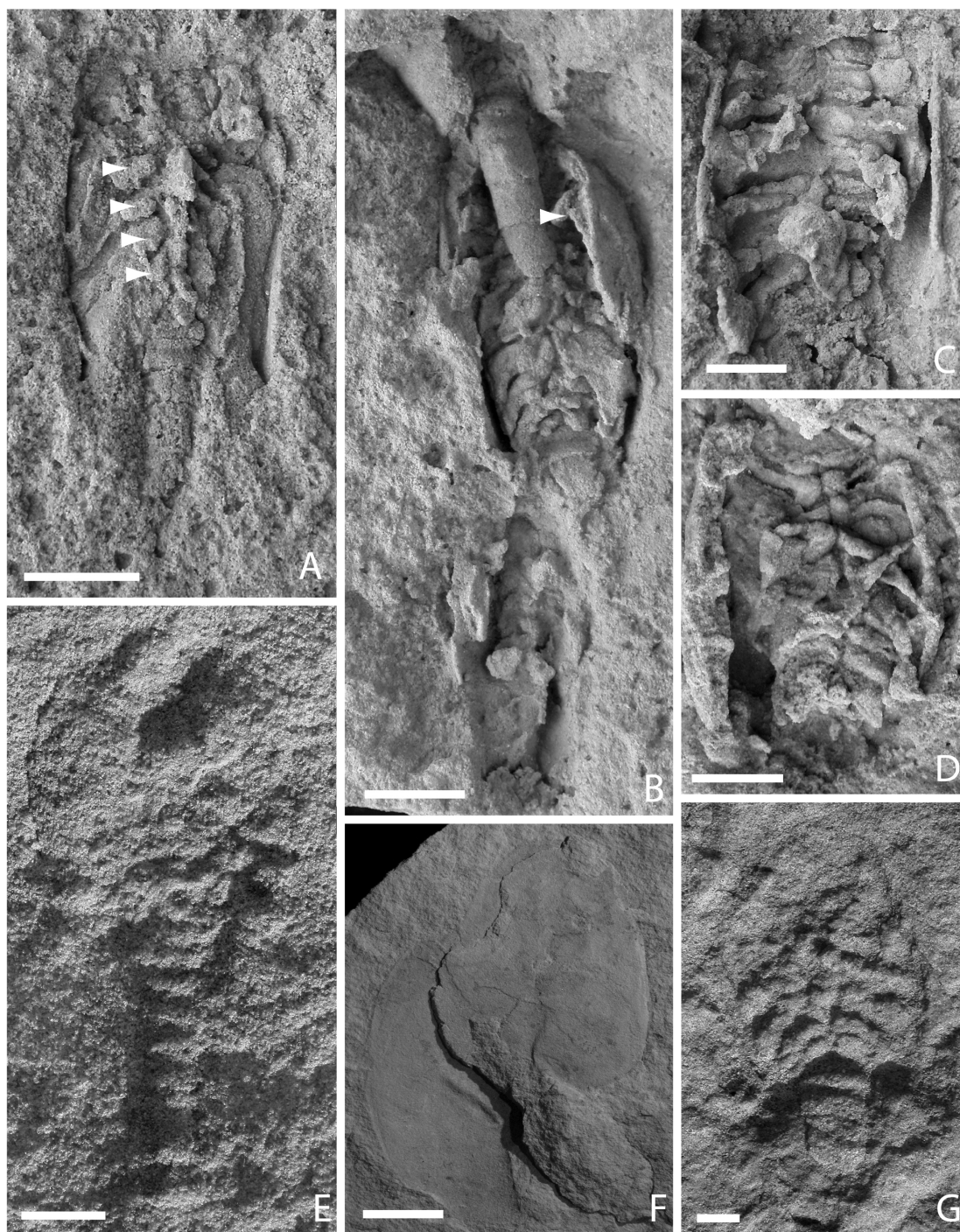


Figure 4. Camera lucida drawings of *Arenocaris inflata* n. gen., n. sp. In all camera lucida drawings where gray is present, gray represents areas of deep relief and white represents areas of high relief. A – PRI 10130 (holotype). This example illustrates abdominal morphology quite well, including details of pleopods. Note also the possible partial impression of a telson at bottom. B – PRI 10131a–c. Specimen shows detail of the exopodites of the pleopods (specimen b, middle), and arrangement of the abdominal somites. Note prominent doublure on the right side of the middle phyllocarid. C – PRI 10131d, showing additional limb morphology. Note apparent ridge present on one protopodite ('r'), and possible thoracopod impressions in the anterior part of the carapace. D – PRI 10132a showing detail of the thoracic appendages. Note closely spaced bulbous proximal limb elements and relatively thin distal limb elements. E – PRI 10142, all seven abdominal somites are present, as well as most of the carapace valves. A very low relief, rounded structure is present in the anterior of this example, representing a possible rostral plate. F – cf. *Arenocaris inflata*, UWGM 745, note thin, well-defined carapace margin. G – Flattened phyllocarid; note the posteriormost two thoracopod pairs are intact, but anterior limbs are spread out and appear partially disarticulated. This example is interpreted as a molt. All scale bars = 1 cm.

Abbreviations used: A1- A7 – abdominal somites; C – carapace; cm – carapace margin; ?co – possible coxa do – doublure; de – distal thoracopod element; en – endopodite; ex – exopodite; p – protopodite; pe – proximal thoracopod limb element; r – ridge present on limb element; th – thoracopod; ?t – possible telson impression.

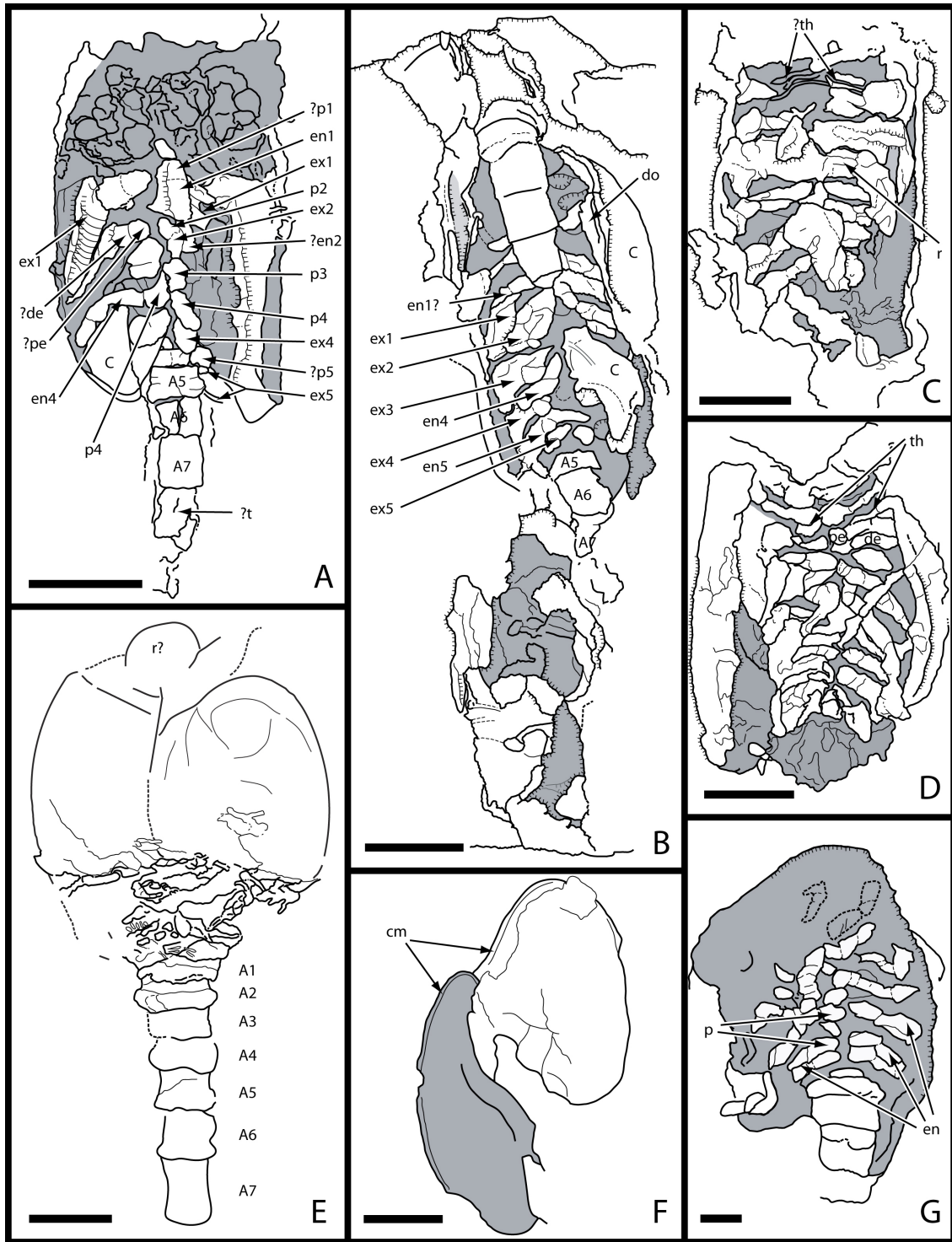


Figure 5. *Mosineia macnaughtoni* and *Mictomerus melochevillensis*. A – PRI 10144 (holotype) *Mosineia macnaughtoni* n. sp. and camera lucida drawing (B). Note that the preservation of the abdominal region is much better than the thoracic region. All six abdominal somites and telson are preserved. Note indistinct imbricate structures present on right side (arrowed ‘i’). C, D – PRI 10145 *Mosineia macnaughtoni* n. sp. and camera lucida. Note the distinct narrow somite separating the thorax and abdomen, and flattened appearance of the abdominal appendages. Seven pairs of flattened limbs are in the thoracic region of this specimen, but note additional structures in the anterior area which may be additional limbs. E, F – ROM 59386 (holotype) *Mictomerus melochevillensis* n. sp. Note that the proximal elements of each limb pair form a ramification, which in turn forms a distinct groove along the ventromedial surface of the arthropod. Note also the five abdominal somites, and that the anteriormost limb on the right side appears to articulate forward. All scale bars = 1 cm. Abbreviations used: A1 – A6 – abdominal segments; ?fa – forward articulation?; gr – ventromedial groove; i – imbricate features; pe – proximal limb element; proximal ramification; t – telson.

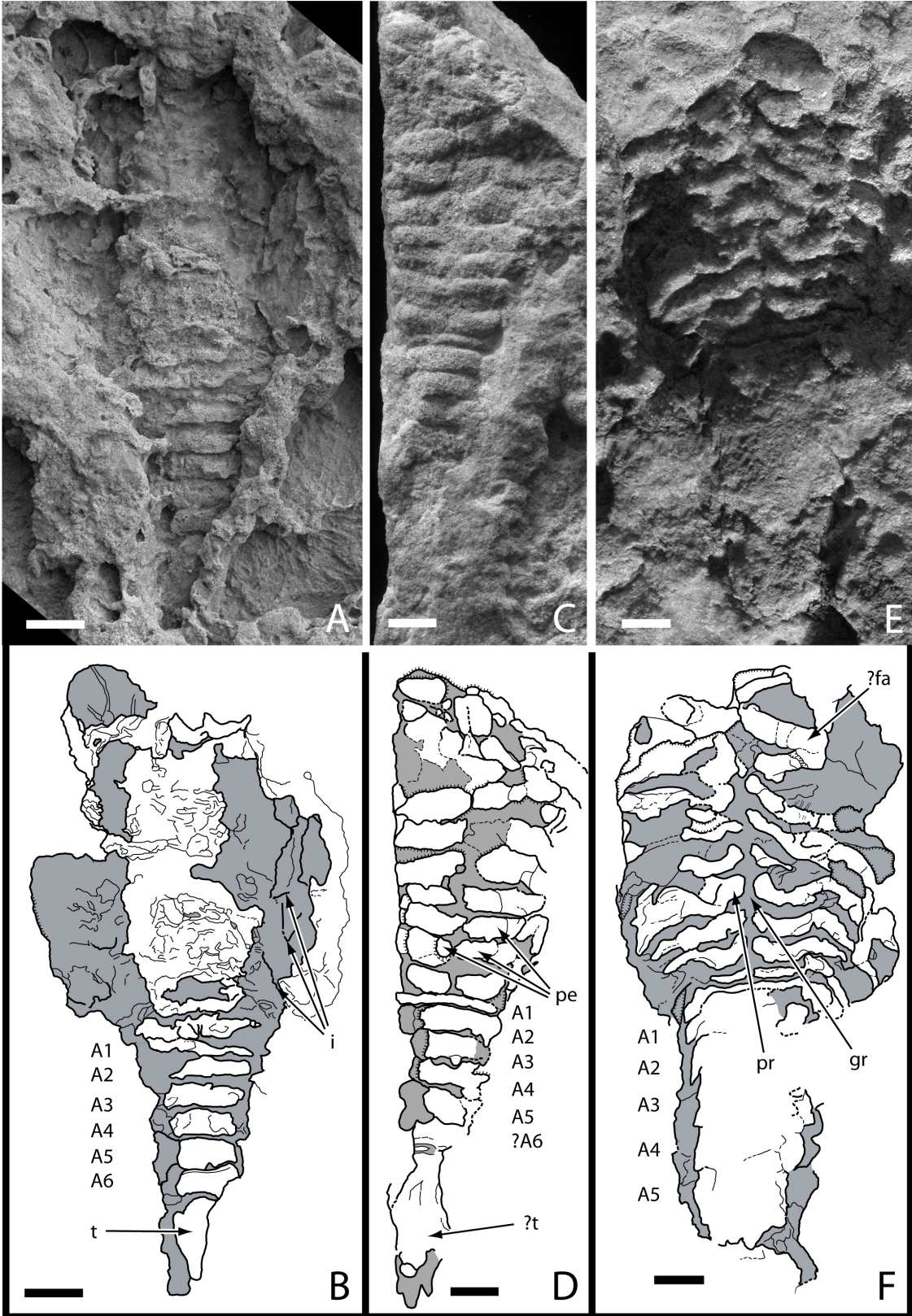


Figure 6. Field photographs of *Mictomerus melochevillensis* from the Potsdam Group.

A – A mostly complete specimen. Note alignment of limbs forming a ventromedial groove. B – Partial specimen revealing detail of the cephalic region. Note anterior convex process extending anterior to the convex cephalic margin (labeled ?hy). C – Partial arthropod showing additional details of the thoracic limbs (vague segmentation) and outline of carapace. D – Nearly complete arthropod showing well-preserved labrum present in the anterior (cephalic) area. Note rear-facing opening present in the labrum. E – Incomplete, poorly preserved specimen showing the shape of the posteriormost tergite. F – Partial arthropod, showing detail of the cephalic area. Note anterior labrum is followed immediately by a pair of appendages. G – Mostly complete specimen showing a clearly defined tergal plate on the left side. Abbreviations used: ap – appendages; hy – possible labrum; pm – posterior margin; te - tergite. All scale bars = 1cm.

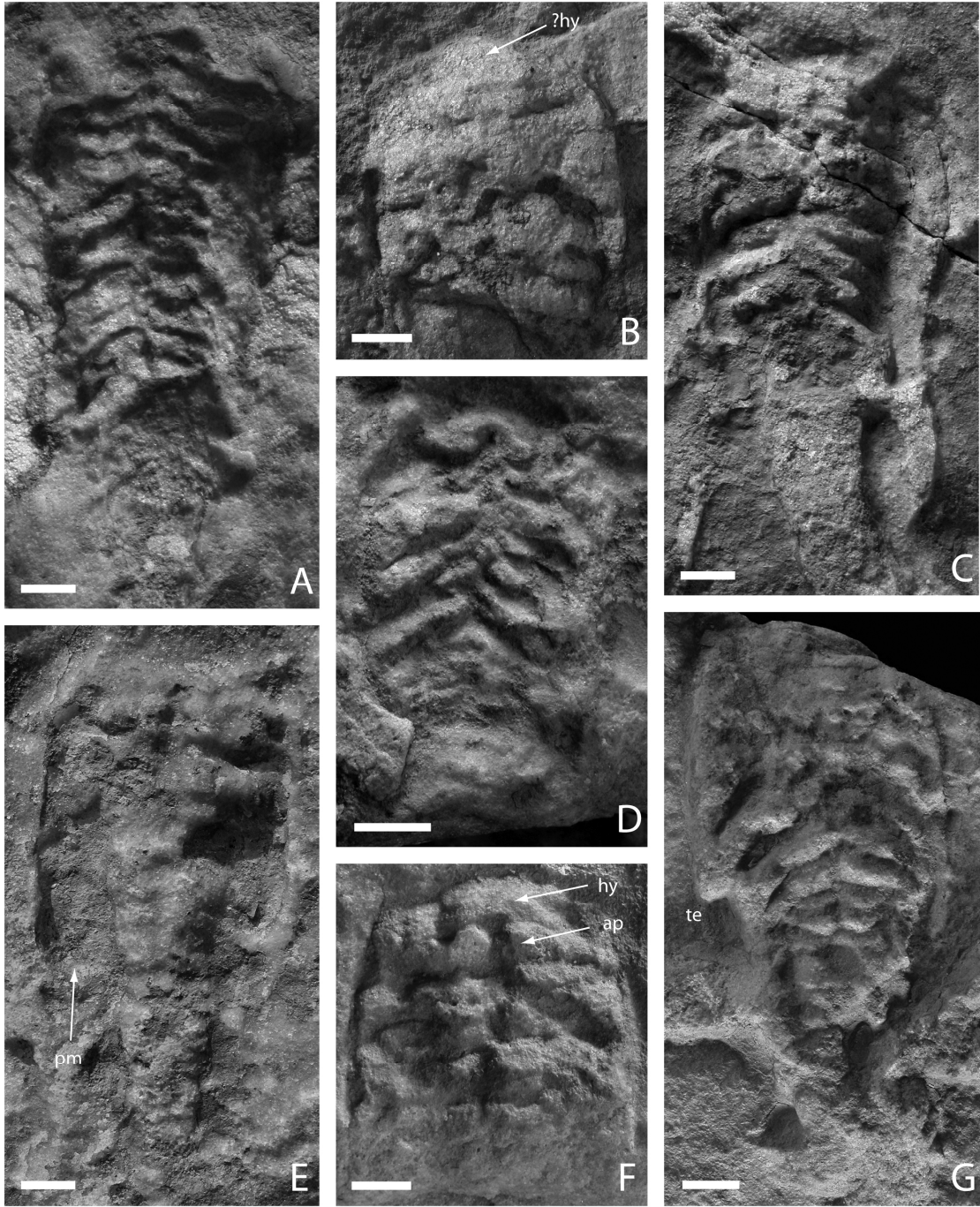


Figure 7. Camera lucida drawings of *M. melochevillensis* shown in Figure 6. A – Note alignment of limbs close to the ventromedial axis forming a ventromedial groove (arrowed ‘g’), and presence of proximal limb elements (arrowed ‘pe’). Partial labrum appears preserved at the anterior margin of the cephalic area. Tergal plates are evident in this specimen, as are at least four apodous abdominal segments. B – Partial arthropod, revealing detail of the cephalic region. The posterolateral margin of at least two dorsal tergal plates are visible (labeled ‘te’ right side), and possible eyes (arrowed ‘?e’). C – Detail of limb tagamization - three limb elements (numbered) may be present. D – Note well-preserved labrum present in the anterior (cephalic) area, with rear-facing opening. Also note limb with five apparent limb elements (numbered). E – Note shape of the posteriormost tergite and the apparent invagination of one of the posterior abdominal somites – possibly representing an anus. F – Cephalic area showing arrangement of the labrum and anteriormost pair of appendages. Note laterally located, round, globular structures, interpreted as ventrolaterally located eyes. G – Nearly complete arthropod showing a clearly defined tergal plate on the left side, and several apparent tergites on the right. All scale bars = 1cm. Abbreviations used: ?a – possible anus; ap – anterior appendage pair; A1 – A4 – abdominal segments; e – eye; g – ventromedial groove; hy – labrum; pe – proximal limb element; pm – tergite posterior margin; te – tergite.

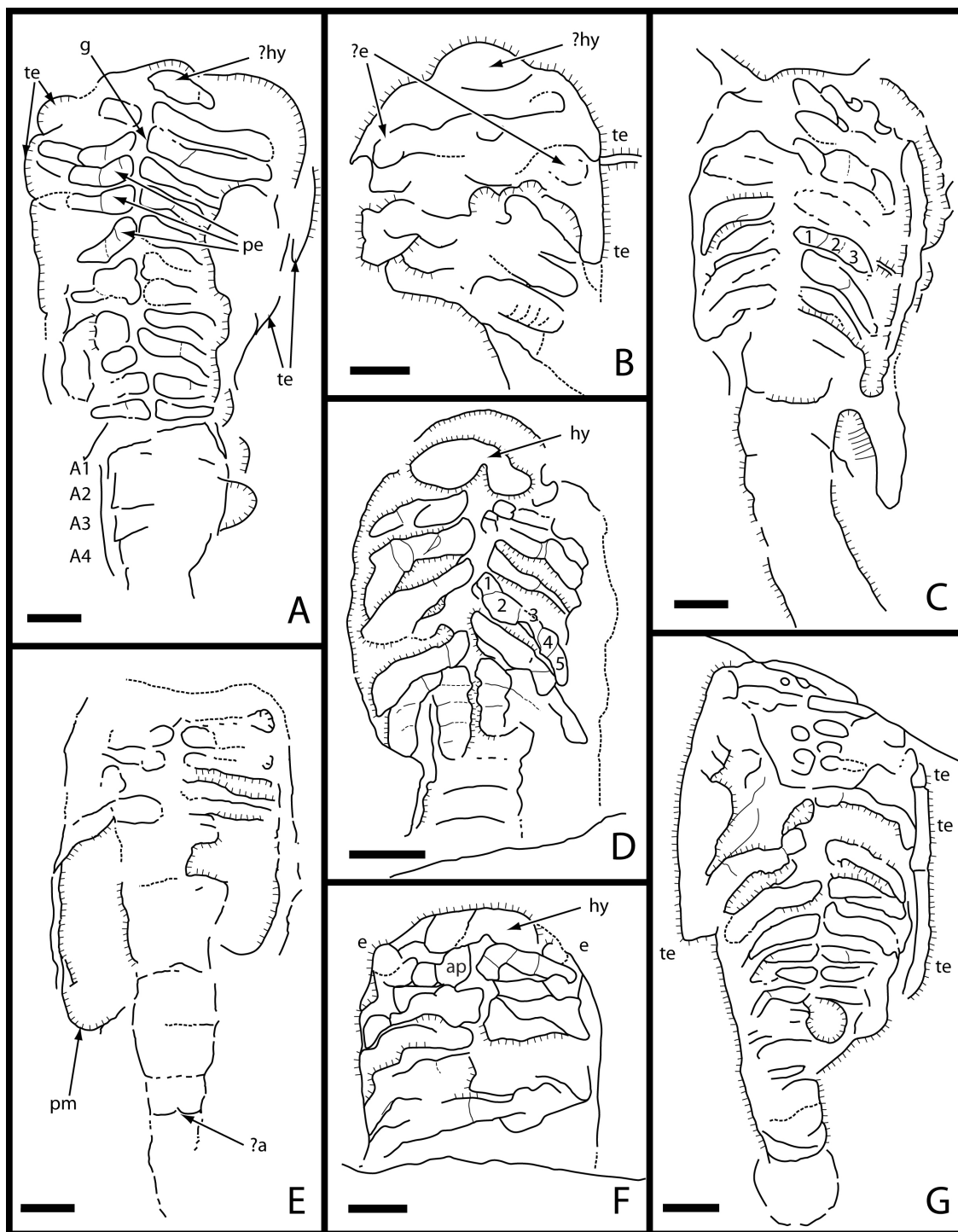


Figure 8. Field photographs and camera lucida drawings of *M. melochevillensis*. A, B – Specimen showing general outline of the thoracic area. Note also presence of at least four apodous abdominal somites (numbered). Note possible eye in the right anterior portion of the cephalic area. C, D – Specimen showing exceptionally well-preserved limbs. Note gradual decrease in overall limb size posteriorly, and the limited limb tagmatization (numbered). E, F – Specimen showing imbricated, slightly convex tergites on the right side. An additional tergite is present in the upper left side of the drawing. This example also preserves at least four abdominal somites (numbered). All scale bars = 1 cm. Abbreviations used: A1 – A5 – abdominal segments; te – tergite.

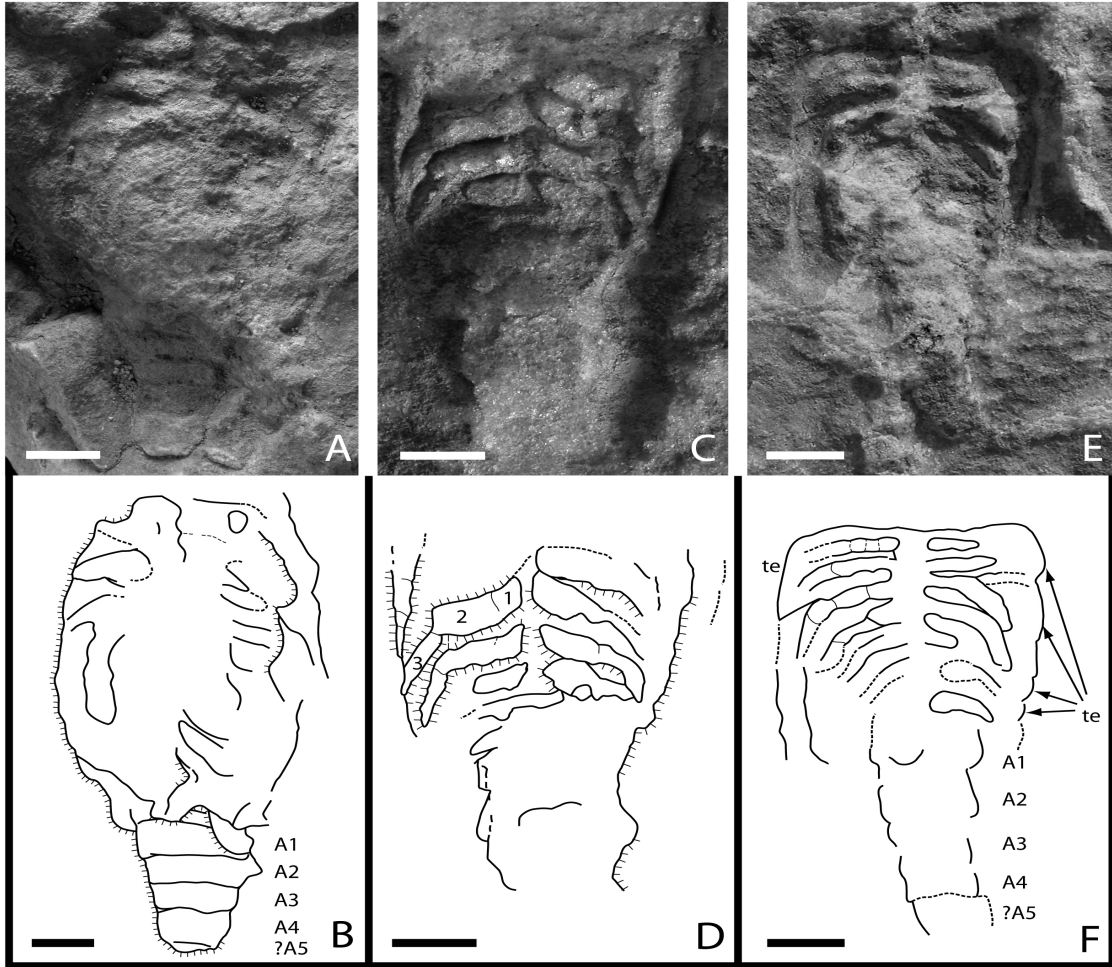
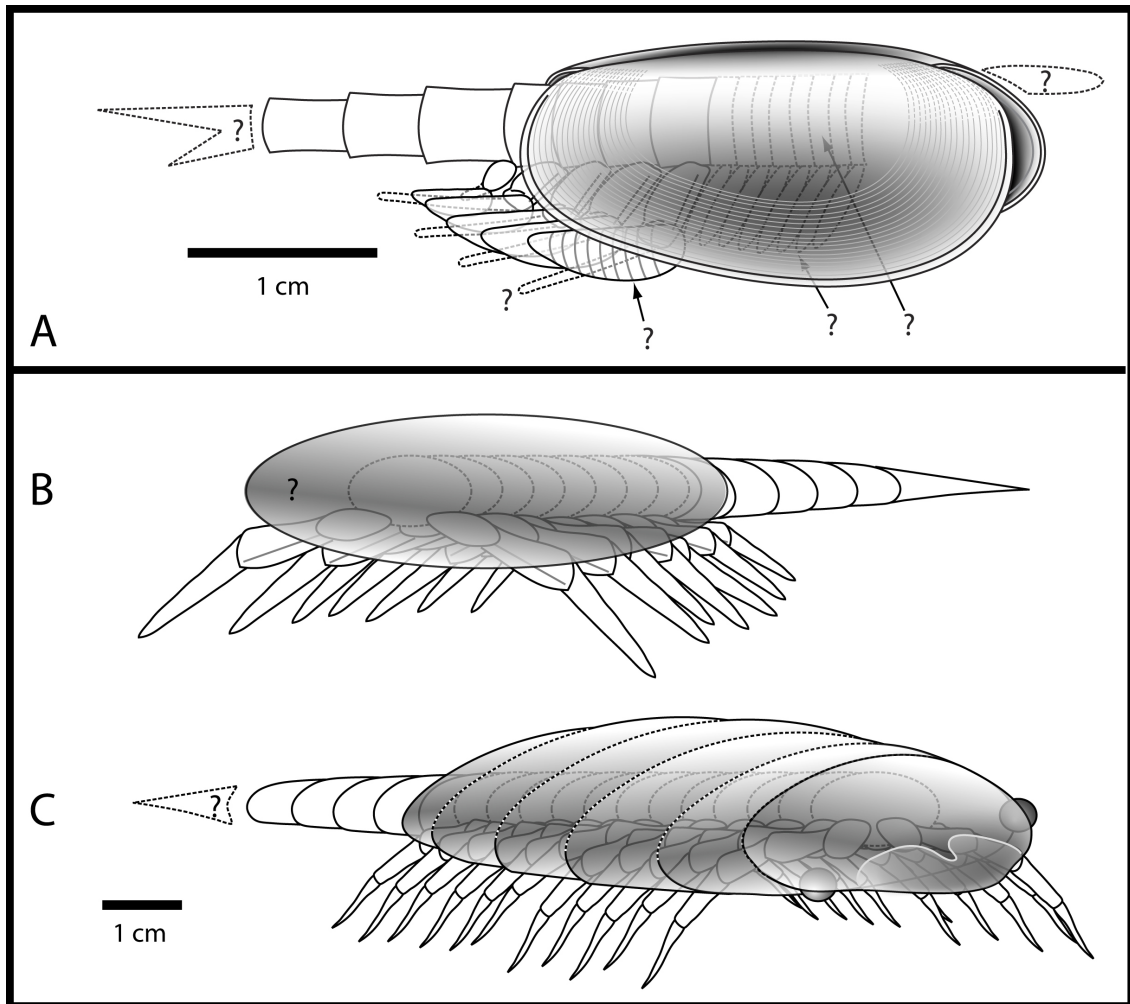


Figure 9. Reconstructions of the arthropods presented in this study. A – *Arenocaris inflata* n. sp. from the Elk Mound Group and Lodi Member, St. Lawrence Formation of Wisconsin. Reconstruction based on 47 specimens. B – Reconstruction of *Mosineia macnaughtoni* n. sp. from the Elk Mound Group of Wisconsin. Reconstruction based on 3 specimens. C – Reconstruction of *Mictomerus melochevillensis* n. sp. from the Cambrian intertidal Potsdam Group of southern Quebec. Reconstruction based on 30 specimens. Dashed lines and question marks indicate areas that are currently not known with sufficient detail to reconstruct. Scale bar represents specimens of average size.



CHAPTER 2.

EARLY EVOLUTION OF PHYLLOCARID ARTHROPODS: PHYLOGENY AND SYSTEMATICS OF CAMBRO-DEVONIAN ARCHAEOSTRACANS AND LEPTOSTRACANS

Introduction

Representatives of the Subclass Phyllocarida are important in arthropod systematics and the early evolution of crustaceans. Phyllocarids are malacostracan crustaceans that possess a bivalved carapace (with or without dorsal hinge line), eight limb-bearing thoracic somites, an abdomen of seven somites (five to six bearing limbs) terminating in a telson, and generally, furcal rami. Phyllocarids are divided into two orders, the extinct Archaeostraca (can be substantial size, five limb-bearing abdominal somites, carapace with hinge line, telson produced into elongate structure located medially between two lateral furcal rami) and the Permian to recent Leptostraca (small size, six limb-bearing abdominal somites, carapace without hinge line, telson not produced into medial process between lateral furcal rami (Rolfe, 1969). Phyllocarids are important because they are morphologically quite varied, have lived for at least 510 million years, the order Archaeostraca has an extensive fossil record, and the order Leptostraca is extant with some 10 genera and 39 species distributed worldwide; thus allowing evolutionary trends to be evaluated in substantial detail with both morphology- and molecular systematic approaches. Additionally, easily recognizable species with known ranges may be biostratigraphically useful.

Representatives of the Phyllocarida have recently been documented in the Furongian (Late Cambrian), pushing back the earliest occurrence of this malacostracan group by as much as 20 million years (Collette and Hagadorn, 2008). These fossils occur in intertidal facies, suggesting that by ca. 500 million years ago, this group had already moved into an ecological niche that a substantial portion of modern leptostracan species still inhabit today. Although groups with superficially similar morphologies to the Phyllocarida (i.e. – *Canadaspis*, *Kunmingella*, *Odaraia*, *Waptia*) are known from the Middle Cambrian Burgess Shale and Early Cambrian Chengjiang Lagerstätten, they are excluded from the Phyllocarida because of substantial morphological disparities (Dahl, 1984; Hou and Bergström, 1997; Walossek, 1999).

The monophyly of the Malacostraca has been called into question based on suggestions that the Leptostraca (+ Archaeostraca) are a sister group to the Malacostraca (Schram and Hof, 1998); that the Leptostraca is a sister group to the Cephalocarida (Wills, 1998); and that the Peracarida (e.g., amphipods) are paraphyletic (Watling, 1999), all of which result in a paraphyletic Malacostraca. It is interesting to note that in all of Schram and Hof's (1998) cladograms in which the extinct Archaeostraca is included, the analyses indicate that the Archaeostraca are more derived than are the Leptostraca. This implies that the ancestor of Archaeostraca arose from the Leptostraca. However, fossil evidence for this relationship is sparse; the earliest known occurrence of the order Leptostraca, *Rhabdouraea bentzi*, occurs in Permian rocks, and is the only known fossil representative of the Order (Schram and Mahlzan, 1984). Several recent studies call into question these paraphyletic hypotheses. Dahl (1987) enumerated the synapomorphies between the Phyllocarida

and the Malacostraca, concluding that the Phyllocarida (defined here as the Leptostraca and Archaeostraca only) are distinctly malacostracan crustaceans. Molecular analyses also support the monophyly of the Malacostraca (Spears and Abele 1998, 1999), indicating a sister-group relationship between the Leptostraca and the Eumalacostraca. Giribet et al. (2005) utilized both morphologic and molecular data, concluding that the monophyly of Malacostraca was supported, and also verifying the sister group relationship between the Leptostraca and Eumalacostraca.

Thus, the systematics within the Archaeostraca are in need of revision, because many species have been named based on fragmentary, isolated specimens, particularly in the Ordovician Family Caryocarididae, and the Silurian Family Ceratiocarididae. Some of this revision has begun; for example Rolfe and Burnaby (1961) synonymized ten Scottish ceratiocaridid species to one, *Ceratiocaris papilio*, and Rolfe (1969) synonymized many more phyllocarid species. Racheboeuf et al. (2000) elevated the Ordovician genus *Caryocaris* to familial level, helping to further refine the concept of Ceratiocarididae. Rode and Lieberman (2002) provided a phylogenetic analysis of the Devonian Suborders Echinocaridina, Pephricaridina, and Rhinocaridina; as well as a much needed revision of these taxa.

An interesting aspect of the subclass Phyllocarida is their diversity through time. Only one species is known from Cambrian rocks (*Arenocaris inflata* Collette and Hagadorn, 2008). However, phyllocarids diversified substantially in the Paleozoic; the Ordovician family Caryocarididae produced at least thirteen named species, and some seventeen unREFERRED taxa (Vannier et al., 2003). Diversification of the phyllocarids continued in the Silurian (earliest representative, *C. silurica* known from the

Ordovician) with the family Ceratiocarididae containing an estimated 70 to 80 named species (Jones and Woodward, 1888; Van Straelen and Schmidt, 1934).

Ceratiocaridids declined in the Devonian as the aristrozoids and then echinocaridids diversified (Rode and Lieberman, 2002). Rhinocaridids also arose in the Devonian, and diversified into the Carboniferous, becoming the second most diverse group of phyllocarids (Rode and Lieberman, 2002).

There is a dearth of phyllocarids in the Mesozoic and Cenozoic, however, and only one example of a fossil leptostracan is known from the Permian (Schram and Mahlzan, 1984). What could account for the disappearance of the Archaeostraca, and a nearly complete lack of fossil Leptostraca, a group that is still extant, reasonably diverse, and is known from the Permian? Because the last archaeostracans are known from the Late Triassic (Rolfe, 1969; Feldmann et al., 2004), it is possibly they were in decline following the end Permian extinction and became extinct during the Triassic. But this does not explain the lack of leptostracan phyllocarids, which are known to have evolved by at least the Permian. One possible explanation is that they inhabited exclusively nearshore, high energy environments. A high energy environment combined with their delicate, lightly-mineralized cuticle might explain this lack of fossils. Indeed, a number of leptostracan taxa are known from nearshore environments today.

This contribution focuses on Cambrian to Silurian representatives of Ceratiocarididae and Caryocarididae. All known examples of common, well-preserved taxa are considered for synonymy, and emended diagnoses are provided for several

previously named and new occurrences. Guidelines are also suggested for naming future phyllocarids that will help to stabilize their systematics.

Morphological characters and morphometric data was collected from specimens housed in the following collections: American Museum of Natural History, AMNH; Czech Geological Survey, ICh; the Czech National Museum, Prague, CNMP; Field Museum, PE; Musée d'Histoire naturelle de Nantes, France, MHNN; Museo de Paleontologia de Córdoba, Argentina, CORD PZ; Museum of Comparative Zoology, Harvard University, HMCZ; New York State Museum, NYSM; Paleontological Research Institution, PRI; Royal Ontario Museum, ROM; Smithsonian Institution, NMNH; University of Wisconsin, Madison Geology Museum, UWGM; Weiss Earth Science Museum, University of Wisconsin-Fox Valley, WESM; and Yale Peabody Museum, YPM.

Methods

Morphology-based characters were surveyed from sixty-nine Cambrian to Silurian representatives of the Order Archaeostraca. Data from Rode and Lieberman (2002), and Briggs et al. (2003) were augmented to include additional character states, and inserted into a master dataset from which a NEXUS file was produced for analysis. Two representatives from the Order Leptostraca were included to test the hypothesis raised by Schram and Hof's (1998) cladograms, in which the Leptostraca was hypothesized to be less derived than the Archaeostraca. A hypothetical ancestor taxon was included as an outgroup to polarize character states in the same manner that

Ceratiocaris praecedens and *C. solenoides* were utilized in Rode and Lieberman (2002). The outgroup taxon was rooted as a monophyletic external node.

Phylogenetic Analyses

This study builds on the previous phylogeny of largely Devonian phyllocarid taxa by Rode and Lieberman (2002). Their character set was constructed to elucidate relationships among Devonian taxa with morphologically complex carapace valves. Of the 54 total characters used in Rode and Lieberman (2002), 46 refer only to the carapace valves; this emphasis on valve morphology results from the fact that valves are often the only part of the phyllocarid preserved. Unfortunately, this character set did not allow elucidation of relationships in less derived taxa (considered herein), because the latter have less pronounced differences in carapace morphology. For example, the less derived, pre-Devonian taxa (this study) were coded for the 54 characters in Rode and Lieberman [(2002) given in Appendix I], and added to the Rode and Lieberman's original taxa and analyzed with PAUP*. This approach resulted in most pre-Devonian taxa collapsing to basal polytomies. Thus, additional characters were needed to elucidate pre-Devonian Archaeostracan relationships (these are given in Appendix I; the complete character matrix is given in Appendix II). These new characters were coded only for taxa in the present study, and required a compound, step-wise process to construct the overall phylogeny of Archaeostraca.

This process began by adding a small number of non-Ceratiocaridina taxa to the 43 taxa used by Rode and Lieberman. These added taxa were phyllocarids with morphologically rich carapaces where details of the abdomen were also known; these

taxa comprise analysis I (detailed procedure below). The remainder of the taxa in this study are members of the suborders Ceratiocaridina and Caryocaridina n. suborder, and were coded with 66 characters (54 characters of Rode and Lieberman plus an additional 12 characters that describe further details of the carapace valves and abdomen); these taxa comprise analyses II and III. Care was taken to ensure that the same procedures were followed during character coding as in Rode and Lieberman (2002), so as to minimize potential sources of error and inaccuracy in our results. Asterisks in the character matrix indicate that a particular character was not used in an analysis (see Appendix II).

Additionally, a thorough literature search was performed for the largely Silurian Ceratiocaridina as well as the Ordovician Caryocaridina n. suborder. Morphological comparisons of a variety of parameters were then done. Because a great many of the diagnoses of ceratiocaridids were vague or missing, emended diagnoses are provided where possible. Synonymy and generic reassignments are listed in Table 1. A visual guide to many of the valid members of the Family Ceratiocarididae is given in Figure 12.

Analysis I – non-Ceratiocaridina

To analyze the non-Ceratiocaridina, we included only the original 54 characters of Rode and Lieberman (2002). All taxa present in the original study were included ($n = 43$), with seven additional taxa added ($n = 50$). Additionally, a hypothetical ancestor was coded to polarize character states; this was included in the analysis as a monophyletic outgroup.

Parsimony analysis.—Phylogenetic analysis was done using PAUP* 4.0b10 (Swofford, 2003). The character set given in Appendix I was subjected to a heuristic search using a stepwise addition sequence with 100 random replications. All characters were unordered, had equal weight, and were parsimony informative; the MulTrees option was in effect. The branch swapping algorithm used for this analysis was Tree-Bisection-Reconnection (TBR). Seventeen most parsimonious trees with a length of 217 steps were retained. The consistency index for these trees was 0.41, the retention index was 0.82, and the rescaled consistency index was 0.33. The strict consensus tree is Figure 10A.

Analysis II – Ceratiocaridina

For the analysis of the Ceratiocaridina, sixteen well-preserved species were included, in which the morphology of both the carapace and abdomen is well known. All 54 characters of Rode and Lieberman (2002) were included in our character set, but an additional nine characters were coded for a total of 63. Of these 63 characters, only 18 were parsimony informative due to the relatively simple nature of the carapace valves in the Ceratiocaridina. All Ceratiocaridina taxa included are from the Silurian or upper Devonian. *Arenocaris inflata* was included as an outgroup to polarize character states (not shown in Figure 10B). Heuristic search settings were identical to those used in Analysis I, with the exception that 10,000 random replications were performed to ensure a thorough search with the reduced parsimony-informative character set. Ten most parsimonious trees with a branch length of 48 steps were recovered. The consistency index (excluding parsimony-uninformative characters) of these trees was

0.57, the retention index was 0.63, and the rescaled consistency index was 0.39. The strict consensus tree is Figure 10B.

Analysis III – Caryocaridina

Seven taxa were included in the analysis of the Caryocaridina. Unfortunately, caryocaridids are almost never usually preserved intact. Thus, characters of the abdomen are, for the most part, unknown; caryocaridids also possess morphologically simple carapace valves. Because of this lack of morphological character information, only five parsimony-informative characters were found within the complete character set ($n = 62$). The heuristic search settings used for this analysis were similar to those used in the other two analyses, except that 100,000 random replications were performed. Additionally, an exhaustive search was performed (which searches all possible trees, but only for limited data sets), with exactly the same results. Six most parsimonious trees with a branch length of 19 steps were recovered. The consistency index (excluding parsimony-uninformative characters) of these trees was 0.89, the retention index was 0.83, and the rescaled consistency index was 0.79. The strict consensus tree is Figure 10C. These three cladograms are combined in Figure 11, a phylogeny of sixty-nine well-known Cambrian to recent phyllocarids.

A phyllocarid composite tree was produced by combining these three phylogenetic analyses together into one large cladogram of well-known taxa. The strict consensus tree presented in Figure 10A was cut apart in Adobe Illustrator at both node 3 and node 23. The cladogram representing the analysis of the Ceratiocarididae (Figure

10B) was inserted where node 3 had been; the analysis of the Caryocarididae (Figure 10C) was inserted where node 23 had been. The assembled supertree is Figure 11.

Discussion

The phylogeny given in Figure 11 generally supports those of both Rode and Lieberman (2002) and Briggs et al. (2003), with some minor differences. For example, by adding representatives of older groups, such as the Caryocarididae, some interesting relationships are elucidated (Figure 10A, Figure 11).

For example, the Caryocarididae do not plot with the Ceratiocaridina, indicating that the Ceratiocarididae as previously defined is paraphyletic. *Cinerocaris* groups with the Caryocarididae, not with the Echinocaridina as had been hypothesized. The earliest known archaeostracan, *Arenocaris inflata* is basal to both the Pephricaridina and Rhinocaridina. Additionally, the common ancestor of the Ceratiocaridina, Pephricaridina, Rhinocaridina and *Arenocaris inflata* appear less derived than the Caryocarididae, indicating that the origins of the Phyllocarida lie farther back in Cambrian time. Interestingly, the two included extant leptostracan taxa arise from a basal polytomy shared with the Ceratiocaridina, Pephricaridina, Rhinocaridina and *Arenocaris inflata*, indicating that the Leptostraca may be less derived than the Caryocaridina and Echinocaridina, and Leptostraca may have shared a common ancestor with the group consisting of Ceratiocaridina, Pephricaridina, Rhinocaridina and *Arenocaris inflata*.

Systematic Paleontology

Subphylum CRUSTACEA

Class MALACOSTRACA Latreille, 1802

Subclass PHYLLOCARIDA Packard, 1879

Order ARCHAEOSTRACA Claus, 1888

Family unassigned

Genus ARENOCARIS Collette and Hagadorn, In review

Type species.—*Arenocaris inflata* Collette and Hagadorn, In review

ARENOCARIS INFLATA Collette and Hagadorn, In review. Figure 13A.

Arenocaris inflata COLLETTE AND HAGADORN, In review, p. xxx, figures 4A–G, 5A–G, 10A.

Types.—Holotype, PRI-10130.

Occurrence. —Elk Mound Group, Furongian (Dresbachian – Franconian), Mosinee, Wisconsin.

Discussion.—With the discovery of *Arenocaris inflata*, the earliest occurrence of the Phyllocarida is now in the Furongian, some 20 million years before the first occurrence of the earliest Ordovician caryocarids. The differences between *Arenocaris* and representatives of the Ordovician Caryocarididae are numerous: *A. inflata* lacks an anterodorsal carapace horn, a process shared by all caryocarids; *A. inflata* does not have a posterodorsal or posteroventral spine, nor spinules of the posterior margin, all of

which caryocarids possess. However, both groups do have a well-developed doublure of the carapace margin.

Life strategies are also quite different between these groups. *Arenocaris inflata* is known only from shallow intertidal sand-dominated settings. Specimens occur articulated, occasionally at the end of muddled surface trails. These very same surface trails have been observed grading into shallow infaunal burrows, indicating that *A. inflata* could burrow in wet sediment and may have been benthic. Caryocarids, in contrast, are not found articulated, their valves are often enrolled, and their abdominal somites and telsons are quite rare. Along with their rather small size, global distribution, and absence of known burrows, it is likely that caryocarids were planktonic, and degraded and disarticulated on their way to the seafloor (Racheboeuf et al., 2000; Chlupáč, 2003; Vannier et al., 2003). Given these disparate lifestyles and the aforementioned major differences in carapace morphology it is possible that these groups are not closely related. While lifestyle alone is not necessarily an indication of relatedness, support for a distant relationship is provided by the current phylogenetic analysis, in which *Arenocaris inflata* is shown to be much less derived than the Ceratiocarididae (see Figures 10A, 11).

Suborder CERATIOCARIDINA Clarke *in* Zittel, 1900

Diagnosis.—Carapace subquadrate to subovate with straight to gently convex hinge line; anterior carapace horn present; ventral thickened carapace margin present.

Rostrum articulated, lacking longitudinal ridge. Medial dorsal plate absent. Eight short

thoracic segments; seven longer abdominal segments; elongated pretelson somite.

Telson longer than furcal rami.

Type genus.—*Ceratiocaris* M'Coy, 1849.

Included taxa.—Ceratiocarididae Salter, 1860.

Discussion.—This suborder has long been problematic, because it lacks distinct, easily identifiable characters on which to base diagnoses. Members of Ceratiocaridina often possess characters that are subtle or gradational; additionally, the extremely thin cuticle of the ceratiocaridid carapace facilitates compaction, compression, abrasion, distortion, and/or removal of selective areas of the carapace valves (Rolfe, 1962).

Because the shape of the carapace valves is often used as a primary taxabase, a new species has typically been named for each new outcrop producing phyllocarid remains attributable to the Ceratiocarididae (Rolfe and Burnaby, 1961). Many species have been erected based solely on isolated telsons, mandibles, and poorly preserved or fragmentary carapace valves [e.g. – *Ceratiocaris longicaudus* Hall, 1863 (telson); *C. gigas* Jones and Woodward, 1888 (telson spine); *C. leesi* Roy, 1935 (mandible)].

Wide-ranging taxa have suffered this fate particularly acutely; for example,

Ceratiocaris papilio is known from Scotland, Ontario, Wisconsin, and Iowa, and has been described from these areas under at least twelve different species names.

However, this synonymy is far from exhaustive: Sixty-five named species (excluding subspecies, subgenera, and 'unique' unREFERRED ceratiocaridid species) are listed in Van Straelen and Schmitz (1934), and thirty-three are given in Jones and Woodward (1888).

Many of these have been synonymized, but work remains to be done (see Table 1 for synonymy discussed in this paper).

Family CERATIOCARIDIDAE Salter, 1860

Genus CERATIOCARIS M'Coy, 1849

Diagnosis.—A genus of Ceratiocarididae distinguished by sinuous posterior carapace margin; carapace cuticle thin. Carapace ornamented with raised ridge ornamentation, roughly parallel to the ventral carapace margin.

Type species.—*Ceratiocaris solenoides* M'Coy, 1849

Other species.—*Ceratiocaris acuminata* HALL, 1859; *C. bohémica* BARRANDE, 1872; *C. cornwallisensis* COPELAND, 1960; *C. crispus* GOURVENNEC ET AL., 1994; *C. praecedens* CLARKE, 1901; *C. maccoyanus* HALL, 1859; *C. macroura* COLLETTE AND RUDKIN, In Press; *C. solenoides* M'COY, 1849; *C. papillio* SALTER IN MURCHISON, 1859; *C. pusilla* MATTHEW, 1889; *C. rubini* PENEAU, 1935.

CERATIOCARIS ACUMINATA Hall, 1859. Figure 13B.

Ceratiocaris acuminata HALL, 1859, p. 422, pl. 84, fig. 6; POHLMAN, 1886, p. 28, pl. 3, fig. 2; JONES AND WOODWARD, 1888, p. 27; STOSE, 1894, p. 369; GRABAU, 1901, p. 227, fig. 159; GRABAU AND SHIMER, 1910, p. 357, fig. 1676.

Types.—Holotype, YPM 22405.

Ceratiocaris aculeata HALL, 1859, p. 422, pl. 80, fig. 10.

Ceratiocaris deweyi HALL, 1852, fig. 160; GRABAU, 1901, p. 227, fig. 160.

Ceratiocaris longicaudus HALL, 1863, p. 73, pl. 1, fig. 7.

Ceratiocaris poduriformis WHITFIELD, 1896, p. 302, pl. 14, fig. 10.

Ceratiocaris (Limnocaris) clarkei RUEDEMANN, 1925 p. 73, pl. 23, fig. 2–4.

Other material examined.— NYSM 9672–74PE; 665, 56573; ROM 43780; YPM 214722–214730, 186706, 209938, 209939, 209968, 209970, 210003, 212400, 212403.

Diagnosis.—*Ceratiocaris* species with closely spaced, occasionally anastomosing raised striations of carapace. Ventral carapace margin narrow; carapace length to depth ratio around 1.70, anterior horn acuminate. Abdominal somites with raised irregularly spaced, anastomosing striations oriented mostly transverse to trunk axis. Furcal rami with a narrow thickened margin along both edges.

Occurrence.—Upper Silurian, Bertie Group, Williamsville Fm, Bed A, Buffalo, New York.

Discussion.—The competitive exclusion principle holds that species competing for limited resources cannot coexist if ecological factors remain constant; one species will outcompete the others leading to dominance of the successful species and extinction or migration to another niche of the remaining species (Hardin, 1960). At least six species of ceratiocaridids have been named from the Silurian Bertie Waterlime of New York. It is unlikely that this number of large, morphologically very similar, sympatric ceratiocaridid species could be compatible because of competition for resources and habitat (Hardin, 1960; Rolfe and Burnaby, 1961).

Many isolated telsons, rami, and abdomens exist from New York that share overall similar morphology with the caudal appendages of *C. acuminata*. Morphometric ratios suggest that the isolated incomplete abdomen of *Ceratiocaris poduriformis* is likely a juvenile instar of *C. acuminata*. *Ceratiocaris deweyi* is an isolated telson that was originally described by Hall as *Onchus deweyi*, a defensive

spine of a fish. *Ceratiocaris aculeata* and *C. deweyi* are both isolated caudal appendages that are similar or indistinguishable from *C. acuminata*, and are suppressed here as junior synonyms of *C. acuminata*. Insertion sites along the lateral margins of *C. acuminata* are not often well-preserved, but YPM 212400 shows that *C. acuminata* did have lateral spines of the telson. YPM 212400 is a nearly complete phyllocarid that has a series of regularly spaced pits toward the tip of the telson shaft [see Figure 13B, inset (arrowed)]. *Ceratiocaris* (*Onchus*) *deweyi* was originally described by Hall (1852), and thus, the name would take precedent over *C. acuminata*. However, because *C. (Onchus) deweyi* was originally misdiagnosed as a fish spine, and because *Ceratiocaris acuminata* is a well-established species, *C. acuminata* is retained in the interest of genus stability, and *C. deweyi* becomes a *nomen oblitum*.

Ceratiocaris clarkei was erected by Ruedemann (1925) to contain a single nearly complete specimen from the Bertie Group of Canandaigua, New York. The original diagnosis was based on carapace morphology alone (carapace was described as ‘short’). The description noted that the surface ornament of this species is indistinguishable from either *C. acuminata* or *C. maccoyanus*. Because the carapace horn in this specimen is acuminate, like *C. acuminata*, and because there is no other morphological difference other than the taphonomic variation in shape of the carapace valves, *C. clarkei* is referred to *Ceratiocaris acuminata*, and *C. clarkei* becomes a synonym of *C. acuminata*.

CERATIOCARIS BOHEMICA Barrande, 1872. Figure 13C.

Ceratiocaris bohemicus BARRANDE, 1872, p. 447, pl. 19, fig. 1–13.

Ceratiocaris (Bohemicaris) bohémica CHLUPÁČ, 1994, p. 14, pl. 1, fig. 1–6;

RACHEBOEUF, 1994, p. 289, text-fig. 3B, 5; GNOLLI AND SERVENTI, 2005, p.

257, fig. 2a–i.

Ceratiocaris docens BARRANDE, 1872, p. 450, pl. 21, fig. 32–35.

Ceratiocaris inaequalis BARRANDE, 1872, p. 452, pl. 19, figs 14–19.

Ceratiocaris tyrannus, JONES AND WOODWARD, 1888, p. 22, pl 3, fig. 2, 5, 6, pl. 4, fig. 4, pl 5, fig 4.

Ceratiocaris gigas JONES AND WOODWARD 1888, p. 24, pl. 3, fig. 1, pl 4, fig. 2.

Ceratiocaris murchisoni LA TOUCHE, 1884, p. 37, pl. 17, fig. 565.

See additional synonymy in Chlupáč, 1994.

Types.—Lectotype CNMP L29456 (figured by Barrande 1872, pl. 19, figs. 1, 2).

L 30024, 32395, 35430, 36428a, 36429, 36430, 36575, 37712, 40580, 43495, >50 un-numbered specimens.

Emended diagnosis.—Ceratiocaridid with very closely spaced, parallel striations of carapace. Abdominal somites with a raised tubercle at the anteroventral shoulder; raised, irregularly spaced, anastomosing longitudinal striations; trigonal- or leaf-like scale ornamentation may be present on anterior shoulders of posterior abdominal somites; ratio of abdominal somite A7:A6 approximately 2.2:1. Telson with three well-developed, sharp dorsal longitudinal ridges; a deep lateral ridge and a wide shallow ventral groove. Telson head with raised, wavy anastomosing striations

grading onto telson shaft. Lateral spines of telson present. Furcal rami with a series of longitudinal striations (after Chlupáč, 1994).

Occurrence. —Upper Silurian Prídolí Formation, Prague.

Discussion.—Although well-preserved carapaces of this species remain elusive, it is firmly established based on many well-preserved abdominal somites, three-dimensionally preserved telsons, and furcal rami.

Chlupáč established the subgenus *Ceratiocaris* (*Bohemiacaris*) to contain this and other ceratiocaridids that had a short carapace without striation; a prolonged, slender seventh abdominal somite; a greatly elongate telson and furcal rami, both with longitudinal ridges; and sculptural elements of the abdomen and telson head (Chlupáč, 1994). The dearth of carapace valves of this species precludes any taxabase that describes the carapace from being easily implemented. However, one example of *C. bohémica* in the collections of the Czech National Museum (L 21193, Figure 13C inset) is nearly complete, allowing confirmation of the presence of typical ceratiocaridid carapace valve ornamentation. The mean length of abdominal somite A7 to A6 is 2.19 ($n = 5$), but this does not warrant erection of a subgenus as other ceratiocaridids have a similar ratio [i.e. *C. papilio*, 1.8 to 1.9; *C. grata*, 2.23 ($n = 6$)], both of which Chlupáč did not include within this subgenus. Because the taxabases on which this genus was erected are either no longer valid (i.e. carapace ornament shown to be present), or are not demonstrably unique to the originally included taxa, this subgenus is considered herein to be invalid, and the taxa included in the subgenus in Chlupáč (1994) are referred to the genus *Ceratiocaris*.

CERATIOCARIS CORNWALLISENSIS Copeland, 1960. Figure 13D.

Ceratiocaris cornwallisensis COPELAND, 1960, p. 49. pl. 8, fig. 1–2, pl. 9, fig. 5.

Ceratiocaris cornwallisensis damesi CHLUPÁČ, 1963, p. 104, pl. 12, fig. 9–10, pl. 14, fig. 3–5, pl. 15, fig. 1–4, text fig. 3–5.

Ceratiocaris (Ceratiocaris) cornwallisensis damesi CHLUPÁČ, 1994, p. 6, pl. 2, fig. 6.

Ceratiocaris damesi NOVÁK, 1886, p. 676.

Types.—Holotype, Geological Survey of Canada GSC 14006; paratypes GSC 14005, 14011.

Other material examined.—L 29510, >50 unnumbered specimens.

Emended diagnosis.—Ceratiocaridid with raised irregular anastomosing ridges on abdomen; ridges perpendicular to body axis at anterior margin of abdominal somites, becoming arcuate and forming acute angle with ventral margin; longitudinal ridges may be present in the dorsal and posterior areas of abdominal somites. Ratio of abdominal somite A7:A6 approximately 2.4:1. Telson with a prominent axial dorsal carina; lateral spines present; ratio of telson:furca approximately 1.44. Furcal rami with a narrow thickened margin along both inner and outer margins (after Copeland, 1960).

Occurrence.—Upper Silurian (Ludlovian), member C, Cape Phillips Formation, northern Cornwallis Island, Canadian Arctic; Upper Silurian (Zone of *Monograptus hercynicus*), Lowest Devonian to Upper Silurian (near the Lochkovian/Pragian boundary), Lochkov Formation, Radotín-Limestones facies, Prague Basin.

Discussion.—Czech examples of *C. cornwallisensis* had been mentioned by both Barrande and Novak (1886), but never figured or described. Chlupáč erected a new subspecies to contain the Czech material based on very slight morphological

differences: the ratio of abdominal somite A7:A6 is slightly less in Canadian material than in Czech specimens; the ratio of telson:furca is slightly different; and the cross-sectional profile of the telson is different (Chlupáč, 1963). Telescoping of abdominal somites and slight disarticulation adequately explain such small differences in the given ratios; similarly, cross-sections of telsons are often quite different from specimen to specimen. Chlupáč (1963) noted that these differences are not of great importance, and that the difference in the ratio of A7:A6 was due to a measurement error by Copeland in his holotype. No morphological disparity was found between these animals, and the Czech material is referred to *Ceratiocaris cornwallisensis* Copeland.

Similarities also exist between *C. cornwallisensis* and the British phyllocarid species *C. ludensis* Woodward, 1871 from Ludlow, England. In measurements taken from Jones and Woodward (1888) plate 1, the ratio of A7:A6 is only 1.86. Additionally, the furcal rami in *C. ludensis* appear to have longitudinal striations, whereas in *C. cornwallisensis*, the rami have a border delimited by only a thickened margin. Thus, *C. ludensis* appears to be a valid ceratiocaridid species differentiated from *C. cornwallisensis* by the possession of longitudinal striations of the furcae, and the ratio of abdominal segments A7:A6. The carapace valves of *C. ludensis* are unknown, and those of *C. cornwallisensis* are only poorly known.

CERATIOCARIS MACCOYANUS Hall, 1859. Figure 14A.

Ceratiocaris maccoyanus HALL, 1859, p. 421, pl. 84, fig. 1–5.

Types.—Holotype, AMNH 2254.

Other material examined.—AMNH 35202; PE 665, 666, 668; YPM 9913.

Diagnosis.—Ceratiocaridid species with closely spaced, raised, parallel striations of the carapace; carapace margin narrow. Anterior carapace horn rounded. Surface of abdominal somites with raised, wavy, anastomosing striations oriented largely transverse to body axis; A7:A6 ratio approximately 2.06. Telson without lateral spines. Furcal rami flattened, with narrow raised margin along both edges; telson:furca ratio approximately 1.59.

Occurrence.— Upper Silurian, Bertie Group, Buffalo, New York.

Discussion.—This rare species of ceratiocaridid shares a number of morphological characters with *C. acuminata*. In both species, the ornamentation of the abdominal somites is oriented largely transverse to the axis of the trunk, the telsons of both species do not appear to possess lateral spines, and the furcal rami are flattened and have a narrow thickened margin on both edges. However, there are diagnostic differences between the two species: the anterior carapace horn is rounded in *C. maccoyanus*, whereas it is acuminate in *C. acuminata*; the ornamentation of the carapace valves in *C. maccoyanus* is closely spaced, concentric, and parallel, but in *C. acuminata* the ornament of the carapace is less uniform, particular in the area of the ventral margin, and occasionally anastomoses.

Both *C. maccoyanus* and *C. acuminata* are large phyllocarids and they share a significant number of morphological characters. It is possible that *Ceratiocaris maccoyanus* is a taphonomic variant of *C. acuminata*, or is a sexually dimorphic form. Sexual dimorphism is known in a number of modern leptostracan phyllocarid species, with both dimorphic structures [e.g. – dimorphic antennae in species of *Nebalia* (Haney and Martin, 2000)] and smaller overall body size in males (Martin et al., 1996).

CERATIOCARIS MACROURA Collette and Rudkin, In Press

Ceratiocaris macroura COLLETTE AND RUDKIN, In Press, p. xxx, fig. 1A–1E.

Ceratiocaris sp. TETRAULT, 2001, p. 136, fig. 44.

Types.—Holotype ROM 49551; paratype ROM 58940.

Other material examined.—ROM 49546, 49547, 49551, 58935, ROM accession number 03E1 (large lot containing unsorted, unidentified specimens).

Diagnosis.—Ceratiocaridid species distinguished by exceptionally long, styliform telson. Furcal rami with linear, longitudinal grooves present; ratio of telson to furcal rami approximately 4.0. Raised scale-like ornamentation may be present adjacent to the anterior, ventral and posterior carapace margins. Anterior ‘optic node’ present. Length to height ratio of carapace approximately 2.0. Abdominal segments ornamented with raised, sub-parallel longitudinal striae that occasionally anastomose.

Occurrence.—Upper Eramosa Formation, Silurian (Wenlockian), Wiarton, Bruce Peninsula, Ontario, Canada.

Discussion.—See Collette and Rudkin (In Review) for a recent discussion of this species.

CERATIOCARIS PAPILIO Salter *in* Murchison, 1859

Ceratiocaris papilio SALTER *IN* MURCHISON, 1859, p. 262, text figure 1; SALTER, 1860,

p. 155–156, text figure 1; WOODWARD, 1865, p. 401–403, pl. 11, fig. 1 & 2;

COLLETTE AND RUDKIN, In Review, p. xxx, fig. 2A–F.

Ceratiocaris stygius (Salter *in* Murchison), SALTER, 1860, p. 156, text figs. 2 & 3.

Ceratiocaris stygia (Salter in Murchison), JONES AND WOODWARD, 1885, p. 394-397, pl. 10, fig. 2 ;1888, p. 38–42, pl. 10, fig. 7; pl. 11, figs. 3 & 7.

Ceratiocaris monroei (Salter in Murchison), WHITFIELD, 1896, p. 301–302, pl. 13, figs. 1–5; pl. 14, figs. 3–8; WATKINS, MEYER, AND COOROUGH, 2007, p. 9–10, figs. 15.4–15.5, 16.1–16.4, 17.1–17.6, 18.1–18.5, 19.1–19.8.

See Rolfe and Burnaby (1961) for additional synonymy.

Types.—Neotype GSM 7479.

Other material examined.—GSM 7479; ROM 58932–34, 58936–39, accession number 03E1 (lot containing unsorted specimens); COC 20119, 20122–23, 20125, 20136, 20140–41, 20163, 20179–80; PE 6270; HMCZ 5994/1–5994/197, 109906, 109911, 109914, 109923, 109925, 109917–18; MPM 30331; two un-numbered specimens in the collection of Jerry Gunderson; material collected by Curt Klug, repositied at the WESM.

Emended Diagnosis.—Ceratiocaridid with three evenly spaced nodes present on right valve. Length to depth ratio of carapace valves approximately 1.8. Surface of abdominal segments covered with rows of overlapping, irregularly repeating chevron-like scales pointing posteriorly. Telson shaft bearing numerous minute lateral spines, furca with longitudinal striae (after Rolfe, 1962).

Occurrence.—Silurian (Wenlock) Lanarkshire, Scotland; Upper Eramosa Formation, Silurian (Wenlock) Bruce Peninsula, Wiarton, Ontario, Canada.

Discussion.—Jones and Woodward (1888) figured a great diversity of ceratiocaridids in the first volume of *British Palaeozoic Phyllopoda*. Many of the 35 species described in this volume, however, represent multiple examples of single

species. *Ceratiocaris papilio* appears to be most closely related to *C. grata* and *C. bohémica*, with which it shares many characters: a carapace margin with a narrow border; closely spaced, non-anastomosing, raised striations that parallel the carapace margin; scale-like ornament of the abdominal somites; a telson possessing lateral spines; and furcal rami with longitudinal striations. *Ceratiocaris papilio* can be distinguished from all other ceratiocaridid species, however, by its three dorsal hinge nodes, and in having nearly the entire surface of all abdominal somites covered with trigonal scale ornament (in both *C. grata*, and *C. bohémica*, the scale ornament of the abdomen is largely constrained to the dorsal portion of the posterior three somites, and in the case of *C. bohémica*, is confined largely to the anterior shoulders of the somites only).

Rolfe (1962) noted that in smaller examples of this species, the furcal rami bear faint striations. Many examples of this species from the Eramosa Formation of Ontario are preserved in exceptional detail, revealing that the furcae have a series of closely spaced parallel striations present on both their dorsal and ventral surfaces (Collette and Rudkin, In Review). The differences in number and placement of these striae between Scottish and Canadian examples of *C. papilio* could be due to differences in taphonomy between these respective localities, environmental factors, or age of the specific animals.

CERATIOCARIS PRAECEDENS Clarke, 1901. Figure 14B.

Ceratiocaris (Limnocaris) praecedens CLARKE, 1901, p. 92–95, pl. 3, figs. 5–10.

Limnocaris praedences GÜRICH, 1929, p. 57.

Types.—Lectotype, NYSM 4179.

Other material examined.—Paralectotypes, NYSM 4182, 4183, 4184.

Diagnosis.—Ceratiocaridid species distinguished by relatively widely-spaced raised, parallel striations of carapace valves. Anterior carapace horn rounded; ventral carapace border narrow. Abdominal somites with raised irregularly spaced, anastomosing striations oriented largely transverse to trunk axis. Furcal rami with a narrow thickened margin along both edges.

Occurrence.—Silurian, Bertie Waterlime Group, Salina beds, Pittsford, New York.

Discussion.—The subgenus *Ceratiocaris (Limnocaris)* was erected by Clarke (1901) to contain ceratiocaridid forms that had a prominent anterior ‘optic node,’ ‘optic tubercle,’ or ‘eye spot’. However, the cuticle of ceratiocaridids is exceptionally thin and in many species, this ‘optic node’ is probably due to the presence of an underlying mandible. In the originally figured material, such a feature is only vaguely suggested (Clarke, 1901), and a re-examination of the type material in the New York State Museum failed to show any significant anterior topographic high. This species is thus retained within the genus *Ceratiocaris*.

Ceratiocaris praecedens occurs in the Bertie Waterlime with both *C. acuminata* and *C. maccoyanus*. Because all three species are large, and have very similar morphology, it is possible that these species are taphonomic variants. The carapace

horn in may be rounded in *C. praecedens*, however, and the striations of the carapace valves are much more widely spaced than in other members of this genus, suggesting specific validity. *Ceratiocaris praecedens* is thus retained as a valid ceratiocaridid species.

CERATIOCARIS PUSILLA Matthew, 1889. Figure 14C, 12D.

Ceratiocaris pusillus MATTHEW, 1889, p. 56, pl. 4, fig. 9; MILLER, 1889, p. 537;

VOGDEN, 1893, p. 378.

Ceratiocaris pusilla JONES, 1890, p. 64; BASSLER, 1915, p. 1390; VAN STRAELEN AND

SCHMITZ, 1934, p. 63; COPELAND, 1957, pl. 67, fig. 1–3.

Rhinocaris pusilla MATTHEW in Jones, 1898, p. 344; MATTHEW in Jones, 1898, p. 43;

MATTHEW in Jones, 1900, p. 404.

Types.—Holotype ROM 22701; hypotypes, Geological Survey of Canada, 13298 and 13298A.

Other material examined. —ROM 22701; HMCZ 6017/3–6017/95.

Emended Diagnosis.—A small species of *Ceratiocaris* with elongate, subovate carapace valves; hinge line straight, ventral carapace margin narrow; carapace horn acuminate. Carapace ornamentation consists of very faint longitudinal striae. Rostrum long and narrow, may have a median longitudinal ridge. Length to depth ratio of carapace valves approximately 2.15. Telson exceptionally long, greater than the length of the carapace valves (after Copeland, 1957).

Occurrence.—Lower Silurian (Llandoveryan), upper Jones Creek Formation, approximately 14 miles northeast of St. John, New Brunswick, Canada.

Discussion.—An interesting small phyllocarid (carapace between 6 – 14 mm in length) with an exceptionally long styliform telson. Only one abdominal somite and the telson appear to extend past the posterior carapace margin. Ceratiocaridid in appearance, with a sinuous posterior margin and a thickened ventral carapace border. A large number of isolated abdomens occur on a single slab (HMCZ 6017). These phyllocarids are preserved as extremely thin carbon films, thus details of their segmentation and surface sculpture are vague. Abdomens are generally preserved as ‘units’ of 3 or 4 abdominal somites with telson. No abdominal ornamentation occurs on any of these isolated abdomens. The abdominal assembly (including telson) is extremely long relative to the carapace length (>20 mm), approximately 1.6 times as long as the carapace. In the very few specimens that appear to be articulated (HMCZ 6017/95; ROM 22701), only a very short portion of abdominal somite A7 extends past the posterior carapace margin.

Copeland (1957) figured a restoration of *Ceratiocaris pusilla* in which two lateral rami are articulated with the telson. Despite this study’s examination of nearly one hundred specimens of this taxon at the Harvard Museum of Comparative Zoology, Copeland’s reconstruction remains unverifiable and at odds with the available material. It is possible that Copeland (1957) mistook superimposed telsons for a single telson/furca unit, and subsequently based his reconstruction on this artifact. The small size of this phyllocarid, together with the accumulation of oriented abdomens seen in numerous examples, suggests that *C. pusilla* may have had a planktonic lifestyle.

CERATIOCARIS SILURICA Ruedemann, 1934. Figure 14G.

Caryocaris silurica RUEDEMANN, 1934, p. 95, pl. 22, figs. 15–20.

Caryocaris silicula BASSLER, 1919, p. 372, pl. 52, figs 21–23; RUEDEMANN, 1934, p. 92, pl. 23, figs. 7–9.

Types.—Syntype, NMNH 66182.

Emended Diagnosis.—A small species of *Ceratiocaris* with elongate, ovate carapace valves; hinge line straight, becoming gently convex anteriorly. Ventral carapace margin wider in the anterior one-third of valve, narrows posteriorly; carapace horn short, bluntly rounded. Carapace ornamented with faint longitudinal striae. Carapace length to depth ratio approximately 3.3 (after Ruedemann, 1934).

Occurrence.—Ordovician Martinsburg Shale (Corynoides bed), Strassburg, VA.

Discussion.—This small species of *Ceratiocaris* is interesting because it may be the earliest known member of the genus, and it possesses many characteristics of a planktonic lifestyle, including small size and a narrow elongate carapace. Several features of this phyllocarid are incompatible with placement in the Caryocarididae in which Ruedemann originally placed it: the outline of the carapace with well developed sinuous posterior margin, vague longitudinal striae of the carapace, no posterodorsal or posteroventral spines, no spinules on the posterior margin, and telson and rami long and narrow. These features are diagnostic of the Ceratiocaridina genus *Ceratiocaris*, however, to which this taxon is referred. However, many of the earlier members of this genus appear to be small and elongate, suggesting a planktonic lifestyle, and a possible

evolutionary linkage to *Caryocaris*; indeed, many of these small elongate ceratiocarids have been misidentified as caryocarids because of superficial similarities.

CERATIOCARIS SOLENOIDES M'Coy, 1849

Ceratiocaris solenoides M'COY, 1849, p. 413; JONES AND WOODWARD, 1888, p. 52, pl. 8, fig. 4a, 4b, 5, 7a, 7b, 8a, 8b, 9a, 9b, 10a, 10b.

Types.—A type specimen was not assigned in the original description of this species, (M'Coy, 1849); however, two specimens in the collections of the Sedgewick Museum of Earth Sciences, Cambridge University, England are listed as syntypes: A 37180 and A 37181.

Occurrence.—Upper Silurian (Ludlow) Kirkby Moor Formation, Benson Knot, near Kendal, Westmoreland, England.

Discussion.—The type species of *Ceratiocaris* is rather atypical of the genus. It is elongate, with a fairly straight hinge line, and an acutely rounded anterior carapace horn. The posterior margin begins dorsally with a straight, oblique portion that becomes acutely rounded marking the posterior start of the ventral margin. The ventral margin is gently convex, becoming more convex at the anterior end as it grades into the carapace horn. M'Coy (1849) originally described these carapace valves as having an anterior tubercle (i.e. – 'optic node'), but Jones and Woodward (1888) subsequently removed this feature from the diagnosis citing a lack of evidence in numerous specimens examined. No abdominal somites or telsons are known. Because the preceding description was based on lithographs in Jones and Woodward (1888), no emended diagnosis for *C. solenoides* is given.

CERATIOCARIS TELLERI Whitfield, 1896. Figures 14E, 14F.

Entomocaris telleri WHITFIELD, 1896, p. 300, pl. 12.

Types.—Lectotype, AMNH 2620; syntype NMNH 94423, a supposed part and counterpart.

Other material examined.—AMNH 32171–32173; NMNH un-cataloged material.

Occurrence.—Waubeka, Wisconsin. Stratigraphic information not available.

Discussion.—Whitfield (1896) erected the genus *Entomocaris* to contain a single nearly complete phyllocarid from Wisconsin that has rounded anterodorsal and posterior margins. Variation within the thin cuticle carapace valves of ceratiocaridids, however, is a well-known phenomenon (Rolfe and Burnaby 1961; Rolfe, 1962; Rolfe, 1963). In many ceratiocaridid species, where a large number of carapaces of well-defined specific affinity are known (i.e.- *Ceratiocaris acuminata*, *C. papilio*), the within-species range in carapace shape is great. Because all known ceratiocaridids have extremely thin cuticle, using the carapace shape of a single example as a taxabase to define a new genus is artificial. Because the genus *Entomocaris* was erected to contain one individual based on an artificial taxabase, *Entomocaris* is considered a *nomen dubium* and referred to *Ceratiocaris*.

Genus EMMELEZOE Jones and Woodward, 1886. Figure 15I, 15J.

Type species.—*Emmelezoe crassistriata* JONES AND WOODWARD, 1886.

Other species.—*Emmelezoe decora* CLARKE, 1901; *Emmelezoe maccoyiana*, JONES AND WOODWARD, 1886.

Emended Diagnosis.—Carapace subquadrate to subovate; hinge line flat or slightly convex, narrow thickened ventral margin present. Anterior carapace horn present; posterior margin flat or convex. Carapace ornamented with prominent raised, wavy, anastomosing longitudinal striations. Anterior node present; median dorsal plate absent (after Clarke, 1901; Jones and Woodward, 1886).

EMMELEZOE DECORA Clarke, 1901

Emmelzoe decora CLARKE, 1901, p. 95, pl. 2, fig. 4–11, pl. 3, fig. 1–4; GRABAU, 1910, p. 379, fig. 1683.

Gonatocaris decora ROLFE, 1969, p. R316, fig. 138.

Types.—Clarke (1901) did not designate a type specimen in the original description of this species. NYSM 4427 is designated the lectotype; NYSM 4428–4430 and 4434–4436 are designated paralectotypes.

Diagnosis.—Species of *Emmelezoe* with distinct, high relief, anastomosing wrinkle-like longitudinal carapace ornament; smaller-scale anastomosing striae occur in the space between the larger striae. Greatest carapace depth occurs in anterior third of carapace valve. Posterior margin shallowly convex; carapace horn short, acuminate. Abdomen as much as twice carapace length; entire surface of all abdominal somites covered in ovate- to deltoid-shaped scale-like ornament oriented with the sharp end pointing posteriorly.

Occurrence.—Upper Silurian Salina Beds, Eerie Canal, Pitsford, New York.

Discussion.— In the original diagnosis of this genus, Jones and Woodward (1886, 1888) primary taxabase for the recognition of this genus is the presence of an

‘optic tubercle’ in the anterior of the carapace valves. Because this genus is linked by morphological characters to *Ceratiocaris*, and thus, may share the thin carapace responsible for so-called ‘optic nodes’ in a number of ceratiocaridids species, it is prudent to exercise caution in the use of such a taxabase here. The presence of an anterior carapace horn, a flat or gently convex hinge line, a thickened ventral carapace margin, raised striae ornament of the carapace valves, and abdominal scale ornamentation are all synapomorphies that indicate a close relationship between *Emmelezoe* and *Ceratiocaris*. However, the greatly elongate abdomen is a trait not shared with *Ceratiocaris*, and thus, likely represents an apomorphy for *Emmelezoe*. Disarticulated, slender ceratiocaridid-like telsons occur on bedding planes with *E. decora* in the material examined. In one example, three ridges extend longitudinally, forming two low-relief grooves reminiscent of many ceratiocaridid caudal appendages.

Two of the four British species referred to this genus in Jones and Woodward (1888) are clearly much more closely allied to *Ceratiocaris* than to *Emmelezoe*. The type species, *E. elliptica* Jones and Woodward, 1885 (plate 8, fig. 1a and 1b) has a slightly sinuous posterior margin, a rounded anterior carapace horn, and fine parallel carapace ornament, all of which ally it with *Ceratiocaris*, to which Rolfe (1969) referred it. Similarly, *E. tenuistriata*, Jones and Woodward, 1886, (pl. 7, fig. 9a, 9b) is ornamented with very fine parallel striations of the carapace valves, is clearly a ceratiocaridid, and is also referred to *C. elliptica* M’Coy, 1849, from which Jones and Woodward (1886) removed it.

The two remaining species of *Emmelezoe* erected by Jones and Woodward (1886, 1888), *E. crassistriata* and *E. maccoyana* are retained within the genus.

Because *E. crassistriata* was the second species referred to the genus *Emmelezoe* by Jones and Woodward (1886), and it conforms to the emended diagnosis, it is designated here as the type species for the genus *Emmelezoe*.

Genus PUMILOCARIS Racheboeuf, Vannier, and Ortega, 2000

Type species.—*Pumilocaris granulatus*, Racheboeuf, Vannier, and Ortega, 2000.

Included species.—*Ceratiocaris (Limnocaris) salina*, RUEDEMANN, 1916; *Limnocaris(?) salina*, GÜRICH, 1929.

Emended diagnosis.—Small Ceratiocarididae with carapace length to depth ratio <2.5. Carapace elongate; subquadrate to subovate in outline, posterior margin oblique, sinuous. Narrow thickened ventral border present. Carapace valves without surface striae ornament. Raised, prominent dorsal or anterior tubercle may be present (after Racheboeuf et al., 2000).

PUMILOCARIS GRANULOSUS, Racheboeuf, Vannier, and Ortega, 2000.

Pumilocaris granulatus, RACHEBOEUF, VANNIER, AND ORTEGA, 2000, p. 328, fig. 9–10.

Types. —Holotype, CORD PZ 1937, external mould right carapace valve.

Occurrence.—Upper Ordovician (early Caradoc) Las Plantas Formation, occurs with *Climacograptus bicornis*, *Nemagraptus gracilis*, and *Orthograptus* sp., assigned to the *C. bicornis* Zone.

Diagnosis.—Carapace subovate in outline, approximately 2.5 times longer than high; posteroventral margin markedly rounded; posterior margin oblique, weakly

concave; anterior and ventral margins of the carapace with a very narrow border; anterior of right valve with a small node near the dorsal line; anterodorsal section of the free margin straight or weakly concave suggestive of a frontal incisure. Micro-ornamented carapace (e.g. small granulation). No marginal spinosity (Racheboeuf et al., 2000).

See Racheboeuf et al. (2000) for a complete discussion of this species.

PUMILOCARIS SALINA Ruedemann, 1916. Figure 15A.

Ceratiocaris (Limnocris) salina RUEDEMANN, 1916, p. 92, pl. 33, fig. 1–5.

Limnocris ? *salina* GÜRICH, 1929, p. 57, fig. 6.

Types.—Paratypes, NYSM 9678, 9680 (four specimens on a single small slab).

Diagnosis.—Species of *Pumilocaris* with carapace length to depth ratio approximately 3.0. Anterior acutely rounded carapace horn present; posterior margin sinuous. Carapace valves without surface ornament. Raised, prominent anterior tubercle present.

Occurrence.—Ludlovian Vernon Formation (Salina Group, previously known as Pittsford shale), Pittsford, N. Y.

Discussion.—Only a few examples of this little phyllocarid exist, but preservation is fairly good in these known examples. The telson appears to be rather short and bluntly pointed, and is the only portion of the abdomen to protrude past the posterior carapace margin. Ruedemann (1916) noted furcal rami in his original description of this species, but this feature cannot be verified here. Very vague areas of very slightly higher topography are present in the posterior portion of a few examples

that might be the continuation of abdominal somites beneath the carapace valves, but no observable somites have been observed consistent with those figured by Rudemann (1916, pl. 33, fig. 1 and 3). Ruedemann (1916) also noted a filiform posterior border, suggestive of a relationship between *C. salina* and the caryocarids. However, this carapace character was not verified despite examination of all material presently available. The small size of this phyllocarid, its high carapace length to depth ratio, and lack of carapace valve ornamentation are all characters that are at odds with a diagnosis of *Ceratiocaris*. These significant morphological differences indicate that this phyllocarid belongs in a separate genus within the Ceratiocarididae. This species bears a resemblance to *Ceratiocaris solenoides*, the type species of the genus *Ceratiocaris*, in its small size (although *C. solenoides* is slightly larger) and high length to depth ratio of the carapace valves. However, *Ceratiocaris solenoides* has longitudinal striations of the carapace valves (Jones and Woodward, 1888), whereas the valves of *Pumilocaris salina* are unornamented.

Clarke (1901) originally erected *Limnocaris* as a subgenus of *Ceratiocaris* to contain phyllocarids with a prominent ‘eye spot’; Ruedemann (1916) included *P. salina* in this subgenus; Rolfe (1969) synonymized *Limnocaris* with *Ceratiocaris*. However, the presence of an anterior node is not a valid taxabase for larger Ceratiocarididae because the exceptionally thin cuticle of the carapace valves drapes cephalic structures, creating surficial artifacts of these underlying structures (Salter, 1860; Rolfe and Burnaby, 1961; Rolfe 1962). However, the prominence of an anterior tubercle in this small taxon appears valid, because the entire surface of all carapace valves examined are flattened, indicating no mandibles in the area directly beneath the anterior tubercle.

Clarke's (1901) subspecies *Ceratiocaris (Limnocris)* bears the typical ornament of the genus *Ceratiocaris*: raised longitudinal striations of the carapace valves. Because this species' carapace valves are devoid of such ornament, it is referred to the genus *Pumilocaris*, which has a diagnostic lack of longitudinal striae of the carapace valves as a taxabase.

Genus WARNETICARIS Racheboeuf, 1994

Type species.—*Ceratiocaris cenomanense* Tromelin, 1874.

Diagnosis.—Ceratiocarididae characterized by a telson cross-section flattened, sub-semicircular, without dorsal carina. Telson with a pair of weak longitudinal furrows dorsolaterally situated and two pairs of oblique, short, lateral furrows crossing the latero-ventral margin of the telson before midlength. Furcal rami widened, smooth and dorso-ventrally flattened, bearing a longitudinal furrow at their inner margin (Racheboeuf, 1994).

WARNETICARIS CENOMANENSIS Racheboeuf, 1994

Warneticaris cenomanensis RACHEBOEUF, 1994, p. 284, pl. 2, fig. 1–11, pl. 3, fig. 1–

11; GNOLLI AND SERVENTI, 2005, p. 259, fig. 5a–c.

Ceratiocaris cenomanense, TROMELIN, 1874.

Phyllocarid sp., VANNIER AND ABE, 1992, pl. 2, fig. 5-6.

Types.—Lectotype, MHNN.P.147.

Occurrence.—Upper Silurian Le Val Formation 2.5km south, southwest of Chemiré-en-Charnie, Ludlow-Pridoli.

Discussion.—The primary distinction between the genera *Ceratiocaris* and *Warneticaris* is the morphology of the telson. In *Warneticaris* the telson is subcircular in cross-section and does not have a sharp, well-defined dorsal carina (Racheboeuf, 1994). Shallow grooves delineate a series of rounded, lobe-like carinae, one on the dorsal surface of the telson, and two on each side. The two lateral lobate carinae connect to the ventral surface of the telson at an oblique angle. The telsons of *W. cenomanensis* only bear four to five insertion pits for lateral spines.

In erecting the genus *Warneticaris*, Racheboeuf (1994) included *Ceratiocaris grata*. Material in the collections of the Czech National Museum indicates that the dorsal telson surface of *C. grata* bears a distinct raised medial ridge, thus excluding this species from the genus *Warneticaris*. However, in our phylogenetic analysis, *W. cenomanensis* consistently grouped with both *C. grata* and *C. bohémica* (Figure 10B).

WARNETICARIS GRATA Chlupáč, 1984. Figure 15E.

Ceratiocaris grata CHLUPÁČ, 1984, p. 41, pl. 1, fig. 1–2, pl. 2, fig. 1–6, pl. 3, fig. 1–3, pl. 4, fig. 1.

Ceratiocaris (Ceratiocaris) grata CHLUPÁČ, 1994, p. 5, pl. 1, fig. 8.

Types.—Holotype, L 21191.

Other material examined.—L 21192–93, L 22987, and >50 un-numbered specimens in the collections of the Czech National Museum.

Emended diagnosis.—*Warneticaris* with closely spaced, parallel raised striations of carapace. Ventral carapace margin narrow; carapace length to depth ratio approximately 1.8, anterior horn slightly rounded. Most of surface of abdominal

somites A7 and A6, and the dorsal surface of A5 is covered with raised, pointed scale-like ornament; anterior somites with wavy, raised, anastomosing striae oriented perpendicular to body axis on anterior somite borders, grading to acute to nearly longitudinal orientation at ventral surface. Ratio of A7:A6 approximately 2.2; ratio of telson:rami approximately 1.5. Furcal rami with longitudinal striations (after Chlupáč, 1984).

Occurrence.—Upper Silurian Prídolí Formation, *Monograptus transgrediens* Zone, Velká Chirchle, Praha, Czech Republic.

Discussion.—This Czech species appears most closely allied with both *Ceratiocaris papilio* and *Warneticaris cenomanensis*. However, phylogenetic analysis supports a relationship hypothesized by Racheboeuf (1994) with *W. cenomanensis*. Both species possess raised, posteriorly-directed scale-like ornament on the abdominal segments, but in the case of *C. grata*, this ornament appears slightly more acuminate, giving the appearance of more leaf-like scales; the scale ornament in *C. grata* is also more confined, being restricted to the dorsal portions of abdominal somites A5, A6, and A7; whereas in *C. papilio* the ornament continues to at least the dorsal surface of somite A2, and the scales are much more trigonal in shape. Both *W. grata* and *C. papilio* have longitudinal striations of the furcae, but only *C. papilio* appears to have lateral spines of the telson – these structures have not been observed in *C. grata*.

Suborder CARYOCARIDINA n. suborder

Diagnosis.—Elongated carapace, both dorsal and ventral margins convex.

Rostral plate absent; anterior carapace horn forms a distinct, fixed horn-like rostrum.

Very thin, flimsy, weakly or uncalcified carapace; narrow ridge and/or shallow furrow running parallel to ventral margin. Posterodorsal spine present. Posterior margin straight to oblique, typically fringed with a row of minute secondary spinules.

Posteroventral margin with or without posteroventral spine and a few short spinules extending anterior along the posteroventral margin. Distal abdominal segments short; telson short and relatively broad, pointed. Furcal rami leaf-like, spinules or setae may be present on the inner and outer margins of the rami (after Racheboeuf et al., 2000).

Included taxa.—Caryocarididae Racheboeuf, Vannier and Ortega, 2000;
Caryocaris Salter, 1863.

Type genus.—*Caryocaris* Salter, 1863.

Discussion.—Racheboeuf et al., (2000) elevated *Caryocaris* to the family level, and noted significant disparities in telson and furcal rami morphology, length of abdominal segments, carapace horn (an anterior extension of the carapace and not an articulating process), spines and spinules of the posterior carapace valve margin, and the very thin nature of the carapace. All of these morphological characters fall outside of the traditional definition of Ceratiocarididae, as does the restriction of caryocarids to the Ordovician. Additionally, caryocarids lack the parallel or anastomosing striae ornament typical of the ceratiocarid carapace. These substantial differences in morphology warrant a separation of the Caryocarididae from the Ceratiocarididae to produce separate monophyletic suborders. Synapomorphies specific to this clade

include: a ventrally reflected doublure, anterior horn-like rostrum, spines and spinules of the carapace margin, leaf-like furca with sawtooth outer margin, and spinules of the inner and outer rami margins.

Family CARYOCARIDIDAE Racheboeuf, Vannier and Ortega, 2000

Genus CARYOCARIS Salter, 1863

Type species.—*Caryocaris wrightii* Salter, 1863

Other species.—*Caryocaris wrightii* Salter, 1863; *C. acuta* Bulman, 1931; *C. curvilata* Gurley, 1896; *C. cedarbergensis* Whittle, Gabbott, Aldridge, and Theron, 2007; *C. delicatus* Racheboeuf, Vannier and Ortega, 2000; *C. oblongus* Gurley, 1896; *C. stewarti* Jell, 1980; *C. subula* Chlupáč 1970; *C. zhejiangensis* Shen, 1986.

Discussion.—Members of this genus have recently been extensively studied because of their invasion of Ordovician pelagic environment, early planktonic life habit, potential impact on Ordovician food webs, and widespread distribution (Racheboeuf et al., 2000; Chlupáč, 2003; Vannier et al., 2003). Members of this family are not found articulated. Carapace valves are usually flattened or compressed with no trace of abdominal somites, telsons, or furcal rami. What process other than differences in cuticle thickness or composition could be responsible for selectively preserving only part of an organism? Differential transportation could explain the lack of articulated fossils.

Ceratiocaridids were small, with very lightly mineralized (likely phosphatic) soft parts (Vannier et al., 2003). The small, lightweight carapace, long and narrow aspect of the carapace with pointed anterior end, and the broad, leaf like furcae and

telson were likely adaptations for extensive swimming, suggesting a planktonic lifestyle (Racheboeuf et al., 2000; Vannier et al., 2003). Support for this hypothesis is given by sorting in death assemblages of other planktic organisms, where heavier components drop to the seafloor quickly and lighter, or complex-shaped may components drift farther with even a slight current (Johnson, 1960; Kontrovitz, 1975). As small, lightly mineralized pelagic or epipelagic animals die and drift slowly down through the water column, a combination of processes can break down and transport carcasses and components (Brett and Baird, 1986) (Figure 16). Subsurface currents would selectively transport different body parts at different rates, depending on the size, shape, and mass of the parts. Small, flat, low mass parts that are weakly connected with the trunk (such as pleopods, thoracopods, and rami) would be expected to travel furthest; abdomens might travel less distance than the lightest pieces; and carapaces might travel the least distance.

Caryocarids have long been regarded as planktonic organisms (Ruedemann, 1934; Størmer, 1937; Chlupáč, 1970; Chlupáč, 2003; Vannier et al., 2003). Chlupáč (1970) considered caryocarids as being of likely epibenthic origin, although not necessarily as full-time swimmers, but dwelling in surface mats of algal thalli. Unfortunately, no evidence of algal mats has been found in conjunction with *Caryocaris* remains (Chlupáč, 1970; Chlupáč, 2003). Either of these cases explains the cosmopolitan distribution of the fossil record of the Caryocarididae.

CARYOCARIS CURVILATA Gurley, 1896. Figure 15B, 13C.

Caryocaris curvilatus GURLEY, 1896, p. 87, pl. 4, fig. 3; pl. 5, fig. 3; RUEDEMANN, 1908, p. 488, fig. 469–470.

Caryocaris curvilata CHURKIN, 1966, p. 374, pl. 64, fig. 1, 2; p. 376, pl. 65, fig. 3, 7–9; COPELAND, 1967, p. 1193, pl. 162, fig. 1–5.

Caryocaris cf. curvilineatus RUEDEMANN, 1904, p. 738, pl. 17, fig. 17.

Types.—Syntype, NMNH 8163.

Other material examined.—Hypotypes: NMNH 90857, 90858, 144743, 147441–147454

Diagnosis.—Caryocarididae with oval to subquadrate carapace valves, posterior margin truncated perpendicular to hinge line; length:width ratio 3.1 to 3.2.

Posteroventral spine present. Anterior rostral process relatively short, continues anterior in line with longitudinal body axis.

Occurrence.—Cambrian(?), Canadian Shale, Summit, Nevada; Ordovician (Arenig – Llanvirn) Road River Formation, Alaska; Lower Ordovician graptolitic shale, near Trail Creek (Hailey Creek quadrangle), Idaho.

Discussion.—Some authors have placed *C. curvilata* in synonymy with *C. maccoyi* Etheridge. Braddy et al. (2004, table 25.2, p. 258), listed this species in synonymy with *C. maccoyi* in table 25.2, p. 258; Rolfe (1969, p. R316), also considered *C. curvilata* to be a junior synonym of *C. maccoyi*. However, examination of many specimens of both species reveals subtle differences in carapace morphology, indicating two distinct species. Primarily, these differences are manifested in the morphology of the anterior region of the carapace. In *C. curvilata*, the carapace horn is short relative

to the length of the carapace (NMNH 147451 – 8.8%), and tapers rapidly to its anterior terminus. The anterior margin immediately below the carapace horn is smoothly concave, transitioning to smoothly convex. Material described as *Caryocaris maccoyi* is likely polyspecific, and is treated below.

CARYOCARIS STEWARTI Jell, 1980. Figure 15D.

Rhinopterocaris maccoyi, CHAPMAN, 1902, p. 114–117, pl. 18, figs. 9, 16, 17; 1934, p. 112–113, pl. 11, figs. 9–12.

Types.—Holotype, P54285; Paratypes, P54286–54299, National Museum of Victoria, Australia.

Other material examined.—NMNH 102806, 139853–139862.

Emended diagnosis. —Caryocarididae with elliptical carapace valves, posterior margin truncated perpendicular to hinge line; carapace length:width ratio of 2.4 to 2.8. Posterodorsal spine up to 0.15 of total carapace length, slender, continuing curve of dorsal margin. Posterior margin with fringe of very short spinules, approximately 15 total; posteroventral spine present. Anterior rostral process relatively long, continues anteriodorsally at approximately the same angle as anterodorsal carapace margin (after Jell, 1980).

Occurrence.—Lower Ordovician (Middle Tremadoc?), Morabool River, Meredith, Victoria, Australia.

Discussion.—This caryocarid species was erected by Jell (1980) to receive Australian Ordovician examples of *Caryocaris* that otherwise may have been difficult to assign due to past systematic assignments. A previously figured example from

Australia, *Rhinopterocaris maccoyi* Etheridge, 1892 is very similar to this taxon, but previous descriptions and naming problems prevented assignment to this previously named species.

The confusion arose because a species with no elongate rostral process had been provisionally named *Hymenocaris salteri* in M'Coy (1861). However, no description was given at that time. The name was published again by M'Coy (1867, 1874), again, without description. Salter (1863) published a note where he used the name *Caryocaris salteri*, but no description or figures were given. The first description and figures were published by Etheridge (1892), where he moved the species into the genus *Lingulocaris* and changed the species name to *maccoyi* because there was already a species of *Lingulocaris* named *salteriana*. Chapman (1902) later proposed the genus *Rhinopterocaris*, and assigned *Caryocaris* (*Lingulocaris*) *maccoyi* as its first representative. Chapman (1934) next described *Rhinopterocaris maccoyi* from New Zealand. Some of this material had an elongate rostral process, however. *Caryocaris curvilata* is included with *R. maccoyi* in both Chapman (1902) and (1934), and the reason for the creation of the genus *Rhinopterocaris* is vague; Chapman (1902) does not mention an elongate anterior process anywhere in the description. Chlupáč (1970) noted this absence of defining characters between *Caryocaris* and *Rhinopterocaris*, and proposed the presence of an “elongate anterior carapace horn,” as the diagnostic character of *Rhinopterocaris*, which he demoted to the level of subgenus (Chlupáč 1970, p. 54). In the first figured examples (as *L. maccoyi* in Etheridge, 1892), there appears to be no anterior horn in the lithographic plate. However, Chapman (1902) figured a caryocarid (as *Rhinopterocaris maccoyi*) with a prominent anterior process.

Rolfe (1969) assigned *Lingulocaris mcoyi* to *Ceratiocaris*, but because much confusion surrounds the inception of this species, the original Australian examples with a very short anterior rostral process (*Hymenocaris salteri* and *Lingulocaris maccoyi*) are provisionally assigned to *Caryocaris wrighti*, which is known to have a very short anterior rostral process. The material with long, narrow anterior rostral processes (*Rhinopterocaris maccoyi*) is referred to *Caryocaris stewarti* Jell (1980).

CARYOCARIS SUBULA Chlupáč, 1970. Figure 15E, 15F.

Caryocaris (Rhinopterocaris) subula CHLUPÁČ, 1970, p. 55, text fig. 7–9 pl. 5, fig. 1–10, pl. 6, fig. 1–5, pl. 7, fig. 1–7; RACHEBOEUF, VANNIER, AND ORTEGA, 2000, p. 323, text fig. 13B.

Types.—Holotype, ICh 561a.

Other material examined.—Paratypes, ICh 583, 617; more than 100 specimens with catalog numbers between ICh 563 and ICh 765.

Emended diagnosis.—Caryocarididae with subovate carapace valves, posterior margin acutely angled from the dorsal edge anteroventrally at approximately a 60° angle; length to depth ratio approximately 3.6. Ventral carapace border narrow over entire length, separated by a shallow faint line. Posteroventral spine present; posterodorsal spine longer than posteroventral spine; four to five small posteriorly-directed spinules present immediately anterior to the posteroventral spine. Anterior rostral process long, approximately 16.8% of overall carapace length; continues anteroventrally at approximately the same angle as the anterodorsal carapace margin (after Chlupáč, 1970).

Occurrence.—Ordovician (Llandeilo) Dobrotivi Formation, Prague, Czech Republic.

CARYOCARIS WRIGHTI Salter, 1863. Figure 15G, 15H.

Caryocaris wrighti SALTER, 1863, p. 139, fig. 15; JONES AND WOODWARD, 1892, p. 91, pl. 14, figs. 11-15; GURLEY, 1896, p. 87; RUEDEMANN, 1904, pp. 736, 737, fig. 103; RUEDEMANN, 1908, p. 486–488, fig. 482; CHLUPÁČ, 1970, p. 44-52, pl. 1, figs. 1-9; pl. 2, figs. 1-7; pl. 3, figs. 1-9; pl. 4, figs. 1-8; pl. 5, figs. 3-5; text figs. 2-5; CHLUPÁČ, 2003, p. 111, pl. 1, figs. 5-8.

Caryocaris marri HICKS, 1876, p. 138, pl. 9, figs. 4, 6; JONES AND WOODWARD, 1892, p. 92, pl. 14, figs. 16–18; CHAPMAN, 1912, p. 212, pl. 17; CHAPMAN, 1934, p. 110-111, pl. 9, figs. 5–6.

Types.—Hypotype, NMNH 81629.

Other material examined.—Ich 563, 568, 571, 587, 599, 604, 619, 623, 624, 629, 634, 694, 798, 5217, 5238, 5753, and several un-cataloged specimens in the collections of the Czech Geological Survey, Prague.

Diagnosis.—Ceratiocarididae with ovate to subquadrate valves, posterior margin truncated perpendicular to hinge line; length to depth ratio of carapace valves between 2.0 and 2.5. Ventral margin moderately convex, rimmed by a sharply separated ventral border of moderate convexity and constant width. Posterodorsal and posteroventral spines present; approximately thirty minute spinules between the major spines. Anterior rostral process very short, bluntly pointed, without a protracted anterior horn.

Occurrence.—Ordovician Skiddaw Slate (Arenig-Llanvirn), England; relatively common in Ordovician strata of the Prague basin.

Discussion.—See Chlupáč (1970) for a comprehensive treatment of *Caryocaris wrighti*.

Suggestions Regarding the Stability of Phyllocarida

Many of the difficulties associated with the systematics and taxonomy of the subclass Phyllocarida have been illustrated in this review, largely based on examples within the Ceratiocaridina. Problems stem from: i) naming of new species based on isolated caudal appendages, mandibles, or abdomens; ii) analysis of taphonomically altered flimsy, easily compressed lightly- or non-mineralized cuticular carapace valves; iii) placing emphasis on structures that are possibly related to other anatomical features (e.g. – the hypothesized ‘optic node’ has had a particularly acute effect on the Ceratiocaridina); and iv) incomplete synonymization of groups. Whereas many of these problems have become less of an issue in recent decades, nonetheless caution is advocated in the naming of new species because so many species were named in the 19th and 20th centuries that there is the possibility of a pre-existing synonymy. In the interest of stability of the Phyllocarida, the following guidelines are offered:

1. In new taxa, a paleogeographic investigation should be undertaken to assess the possibility of wide-ranging taxa (e.g.- *Ceratiocaris papilio*, *Caryocaris wrighti*) being described from multiple localities as separate species;

2. Small variances in size, shape, or morphology of anatomical parts that are likely to be subject to taphonomic modification should not be used alone as taxabases for the establishment of new species or genera;
3. Isolated individual elements (e.g. - telsons, mandibles, rami, abdominal somites), incomplete, or badly damaged specimens should not be used as the basis for the establishment of a new taxon unless a relationship to other material can be shown, or a significant morphological departure from any other known taxon can be demonstrated.

With the advent of technology allowing instantaneous access and form-based searching of most rare scholarly journals and books from the 19th century and earlier, the problem of access to difficult-to-obtain original descriptions and fragile, valuable, and irreplaceable engravings is rapidly becoming an artefact of the past. Google Books alone opens up opportunities for rapid and thorough searches of synonymy in a myriad of 19th and early 20th century scholarly works. Together with the aforementioned recommendations, these new technological innovations offer the promise of bringing lasting stability to phyllocarid systematics.

Conclusions

The phylogenetic analysis presented here indicates that Ceratiocaridina as traditionally defined is paraphyletic. Systematic analysis of 30 Cambrian to Silurian caryocaridid and ceratiocaridid taxa results in synonymizing them to only 13 taxa. Integrating these taxa into a cladistic analysis of Cambrian to Devonian phyllocarids reveals that *Cinerocaris* groups with the Caryocarididae, not with the Echinocaridina as

had been previously hypothesized. The earliest known archaeostracan, *Arenocaris inflata* is basal to both the Pephricaridina and Rhinocaridina. The common ancestor of the Ceratiocaridina, Pephricaridina, Rhinocaridina and *Arenocaris inflata* appear less derived than the Caryocaridae, indicating that the origins of the Phyllocarida may lie farther back in Cambrian time. Both extant leptostracan taxa arise from a basal polytomy shared with the Ceratiocaridina, Pephricaridina, Rhinocaridina and *Arenocaris inflata*, indicating that the Leptostraca may be less derived than the Caryocaridina and Echinocaridina, and Leptostraca may have shared a common ancestor with the group consisting of Ceratiocaridina, Pephricaridina, Rhinocaridina and *Arenocaris inflata*. Caryocaridina n. suborder is erected to contain the family Caryocarididae; this subordinal elevation of the Caryocarididae results in both the Ceratiocaridina and Caryocaridina being monophyletic. The Ceratiocaridina are composed of four well-defined monophyletic genera; the relationship between the Caryocaridina genera *Caryocaris* and *Cinerocaris* remains to be further investigated. Preliminary cladistic analysis of the Leptostraca suggests they are less derived than the Archaeostraca, implying they share a common ancestor. This implies that the Leptostraca could have much deeper evolutionary roots than is indicated by the fossil record. With only one occurrence (*Rhabdouraea bentzi*), this widespread extant group could have originated as early as the Cambrian.

Table 1. Synonymy of the phyllocarids treated in this paper.

original taxon name	author, date, pub.	new taxon name
<i>Hymenocaris salteri</i>	M'Coy, 1861	<i>Caryocaris wrighti</i>
<i>Lingulocaris maccoyi</i>	Etheridge, 1892	<i>Caryocaris wrighti</i>
<i>Rhinopterocaris maccoyi</i>	Chapman, 1902; 1934	<i>Caryocaris stewarti</i>
<i>Ceratiocaris aculeata</i>	Hall, 1859, p. 422, pl. 80, fig. 10	<i>Ceratiocaris acuminata</i>
<i>Ceratiocaris deweyi</i>	Hall, 1852, fig. 160	<i>Ceratiocaris acuminata</i>
<i>Ceratiocaris longicaudus</i>	Hall, 1863, p. 73, pl. 1, fig. 7	<i>Ceratiocaris acuminata</i>
<i>Ceratiocaris poduriformis</i>	Whitfield, 1896, p. 302, pl. 14, fig. 10	<i>Ceratiocaris acuminata</i>
<i>Ceratiocaris (Limnocaris) clarkei</i>	Ruedemann, 1925 p. 73, pl. 23, fig. 2–4	<i>Ceratiocaris acuminata</i>
<i>Ceratiocaris bohemicus</i>	Barrande, 1872, p. 447, pl. 19, fig. 1–13	<i>Ceratiocaris bohémica</i>
<i>Ceratiocaris (Bohemiacaris) bohémica</i>	Chlupáč, 1994, p. 14, pl. 1, fig. 1–6	<i>Ceratiocaris bohémica</i>
<i>Ceratiocaris docens</i>	Barrande, 1872, p. 450, pl. 21, fig. 32–35	<i>Ceratiocaris bohémica</i>
<i>Ceratiocaris inaequalis</i>	Barrande, 1872, p. 452, pl. 19, figs 14–19.	<i>Ceratiocaris bohémica</i>
<i>Ceratiocaris tyrannus</i>	Jones and Woodward, p. 22, pl 3, fig. 2, 5, 6, pl. 4, fig. 4, pl 5, fig 4	<i>Ceratiocaris bohémica</i>
<i>Ceratiocaris gigas</i>	Jones and Woodward 1888, p. 24, pl. 3, fig. 1, pl 4, fig. 2	<i>Ceratiocaris bohémica</i>
<i>Ceratiocaris murchisoni</i>	La Touche, 1884, p. 37, pl. 17, fig. 565	<i>Ceratiocaris bohémica</i>
<i>Ceratiocaris cornwallisensis damesi</i>	Chlupáč, 1963, p. 104, pl. 12, fig. 9–10, pl. 14, fig 3–5, pl. 15, fig. 1–4, text fig. 3–5	<i>Ceratiocaris cornwallisensis</i>
<i>Ceratiocaris (Ceratiocaris) cornwallisensis damesi</i>	Chlupáč, 1994, p. 6, pl. 2, fig. 6.	<i>Ceratiocaris cornwallisensis</i>
<i>Ceratiocaris damesi</i>	Novák, 1886, p. 676	<i>Ceratiocaris cornwallisensis</i>
<i>Ceratiocaris (Ceratiocaris) grata</i>	Chlupáč, 1994, p. 5, pl. 1, fig. 8	<i>Ceratiocaris grata</i>
<i>Warneticaris grata</i>	Racheboeuf, 1994, p. 289	<i>Ceratiocaris grata</i>
<i>Ceratiocaris stygius</i>	Salter, 1860, p. 156, text figs. 2 & 3	<i>Ceratiocaris papilio</i>
<i>Ceratiocaris stygia</i>	Jones and Woodward, 1885, p. 394–397, pl. 10, fig. 2	<i>Ceratiocaris papilio</i>
<i>Ceratiocaris monroei</i>	Whitfield, 1896, p. 301–302, pl. 13, figs. 1–5; pl. 14	<i>Ceratiocaris papilio</i>

<i>Limnocris praedences</i>	Gürich, 1929, p. 57	<i>Ceratiocris praecedens</i>
<i>Ceratiocris pusillus</i>	Matthew, 1889, p. 56, pl. 4, fig. 9	<i>Ceratiocris pusilla</i>
<i>Ceratiocris pusilla</i>	Jones, 1890, p. 64	<i>Ceratiocris pusilla</i>
<i>Rhinocris pusilla</i>	Matthew, 1898, <i>in</i> Jones, p. 344	<i>Ceratiocris pusilla</i>
<i>Caryocris silurica</i>	Ruedemann, 1934, p. 95, pl. 22, figs. 15–20	<i>Ceratiocris silurica</i>
<i>Caryocris silicula</i>	Bessler, 1919, p. 372, pl. 52, figs 21–23	<i>Ceratiocris silurica</i>
<i>Caryocris silicula</i>	Ruedemann, p. 92, pl. 23, figs. 7–9	<i>Ceratiocris silurica</i>
<i>Ceratiocris cenomanense</i>	Tromelin, 1874.	<i>Warneticaris cenomanensis</i>

Figure 10. Cladograms produced from phyllocarid phylogenetic analyses I to III. A – I. Strict consensus tree of forty-eight archaeostracan and two extant leptostracan taxa. B – II. Strict consensus tree of sixteen Ceratiocaridina taxa. C – III. Strict consensus tree of seven Caryocaridina taxa (n. suborder). See Analyses I – III in text for details.

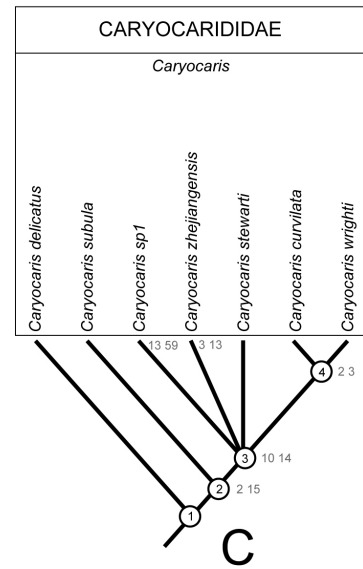
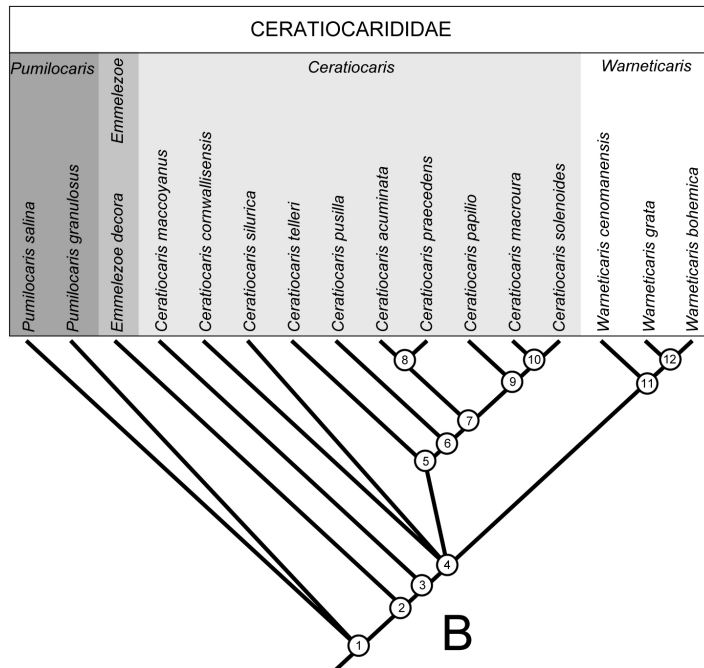
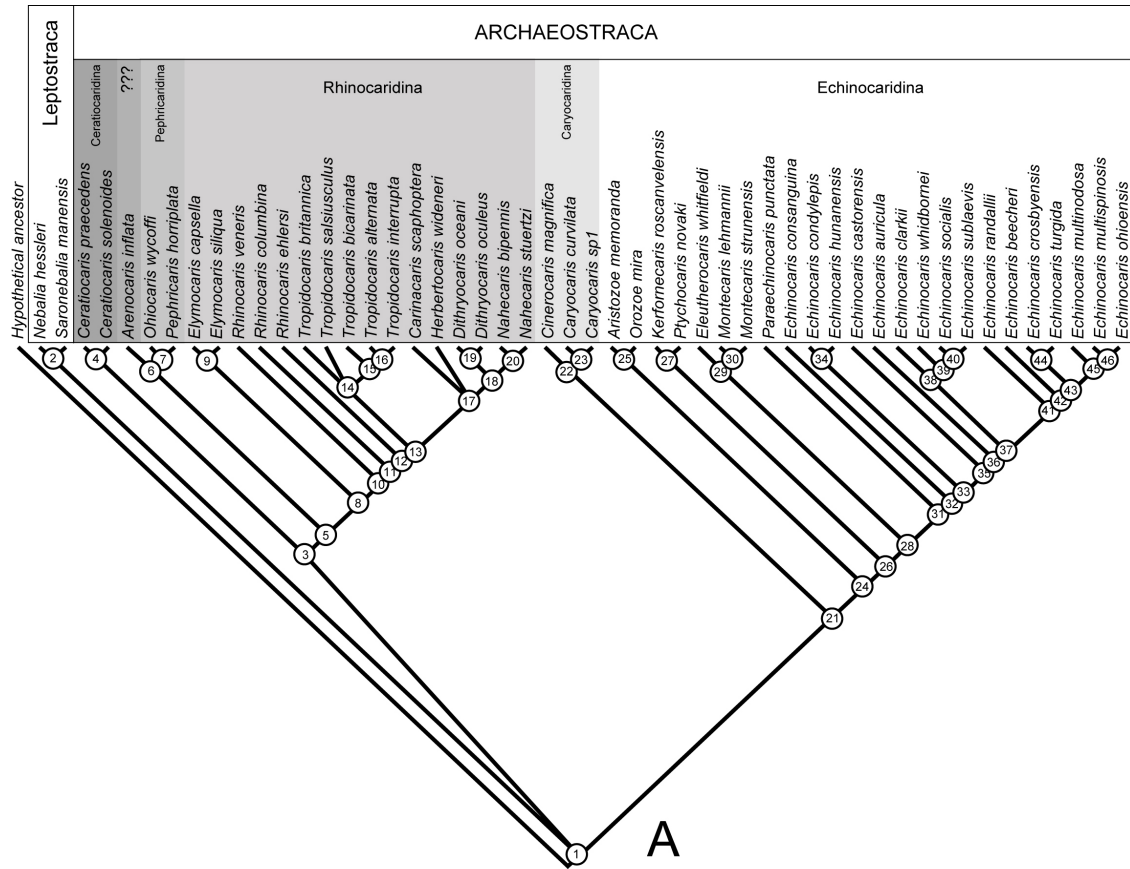


Figure 11. Composite cladogram produced from Figures 10A to 10C. Note the position of the extant leptostracan taxa forming a basal polytomy with branch leading to the Ceratiocaridina, Pephricaridina, and Rhinocaridina. See text for discussion.

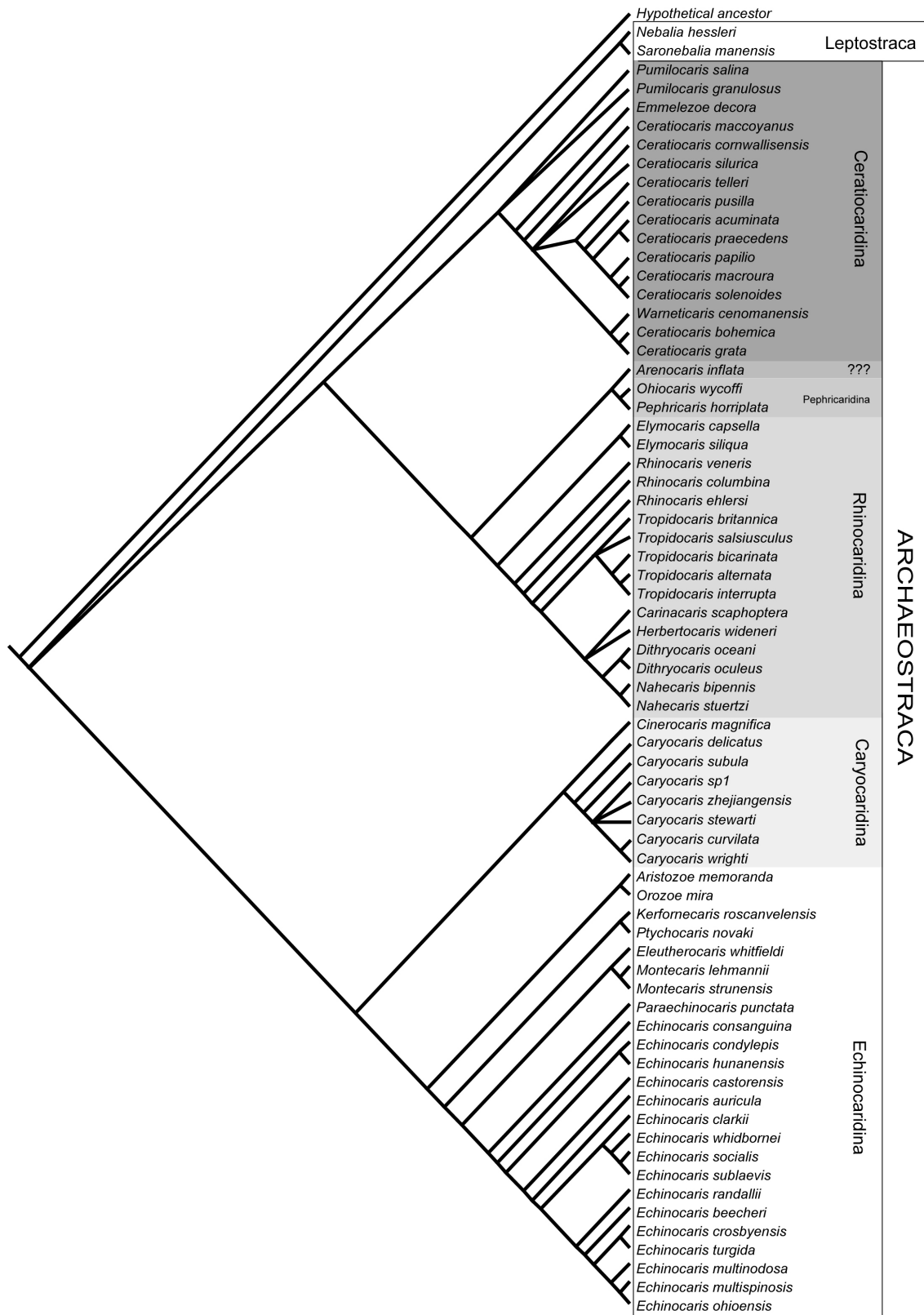


Figure 12. A visual key to members of the Family Ceratiocarididae. Diagrammatic representations of species treated in this paper, and include all parameters of individual taxa as known. If morphometric ratios are known for a taxon, they are also given. Dashed lines and question marks indicate areas that are unknown. Thoracic somites are shown as an approximation of the anterior extent of the trunk only, they are not meant to represent any morphometric parameters. Where telson cross-sectional profiles are known, they are also included.

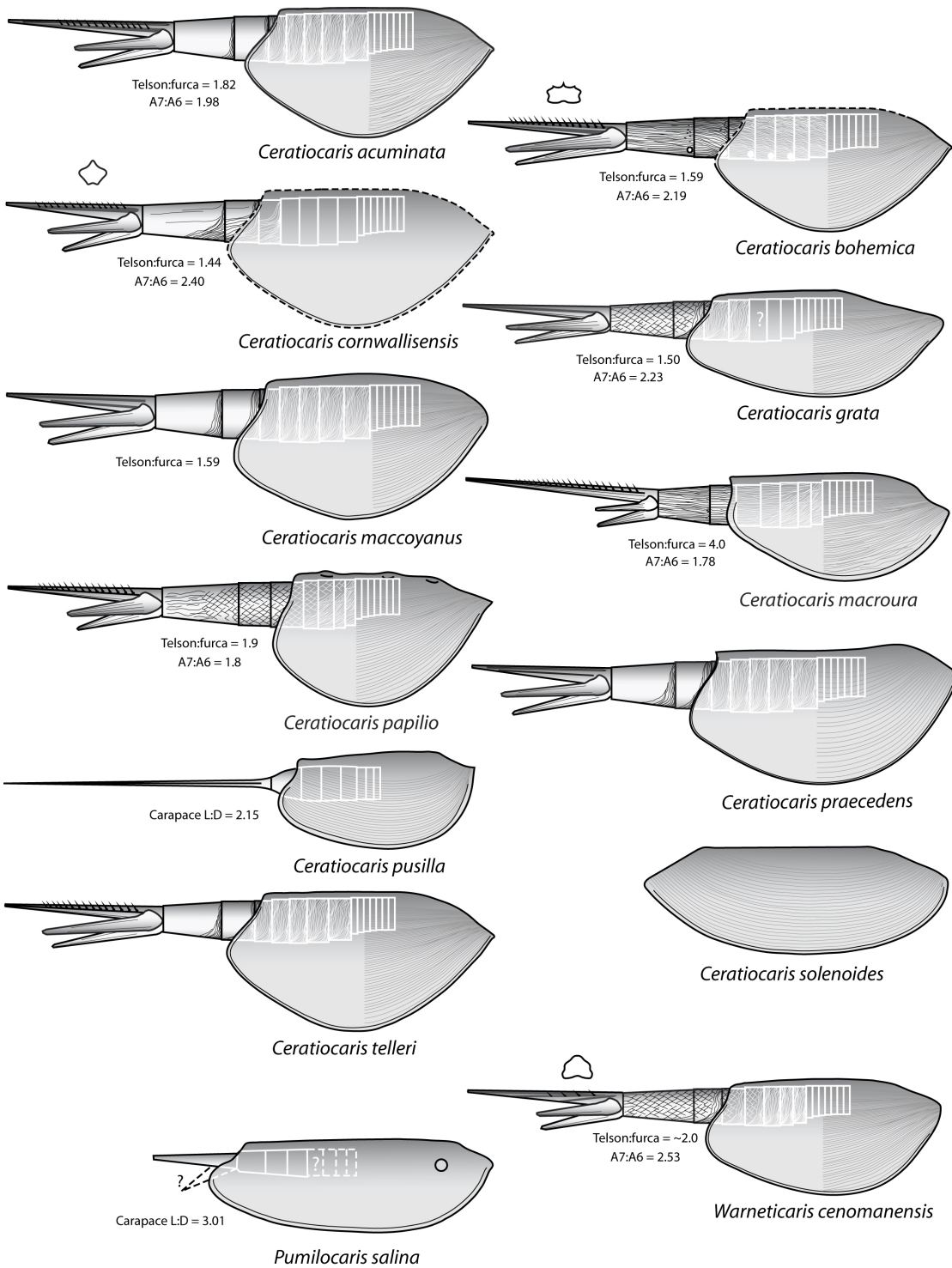


Figure 13. *Arenocaris inflata* and members of the genus *Ceratiocaris*. A - *Arenocaris inflata* from the Furongian Elk Mound Group of Wisconsin – PRI-10131a–c (a at top, c at bottom), 3 phyllocarids; 2 partial, and one complete. B – *Ceratiocaris acuminata*, P-664. Inset image (YPM 212400) shows a telson with a row of vague pits where lateral spines inserted (arrowed). C – *C. bohémica*, L 40580. Inset image shows a nearly complete carapace valve, L 37712. D – *C. cornwallisensis*, un-numbered telson in the collections of the Czech National Museum, Prague. E. – *Warneticaris grata*, L 37712, a rare carapace valve showing ornamentation. All scale bars = 1 cm.

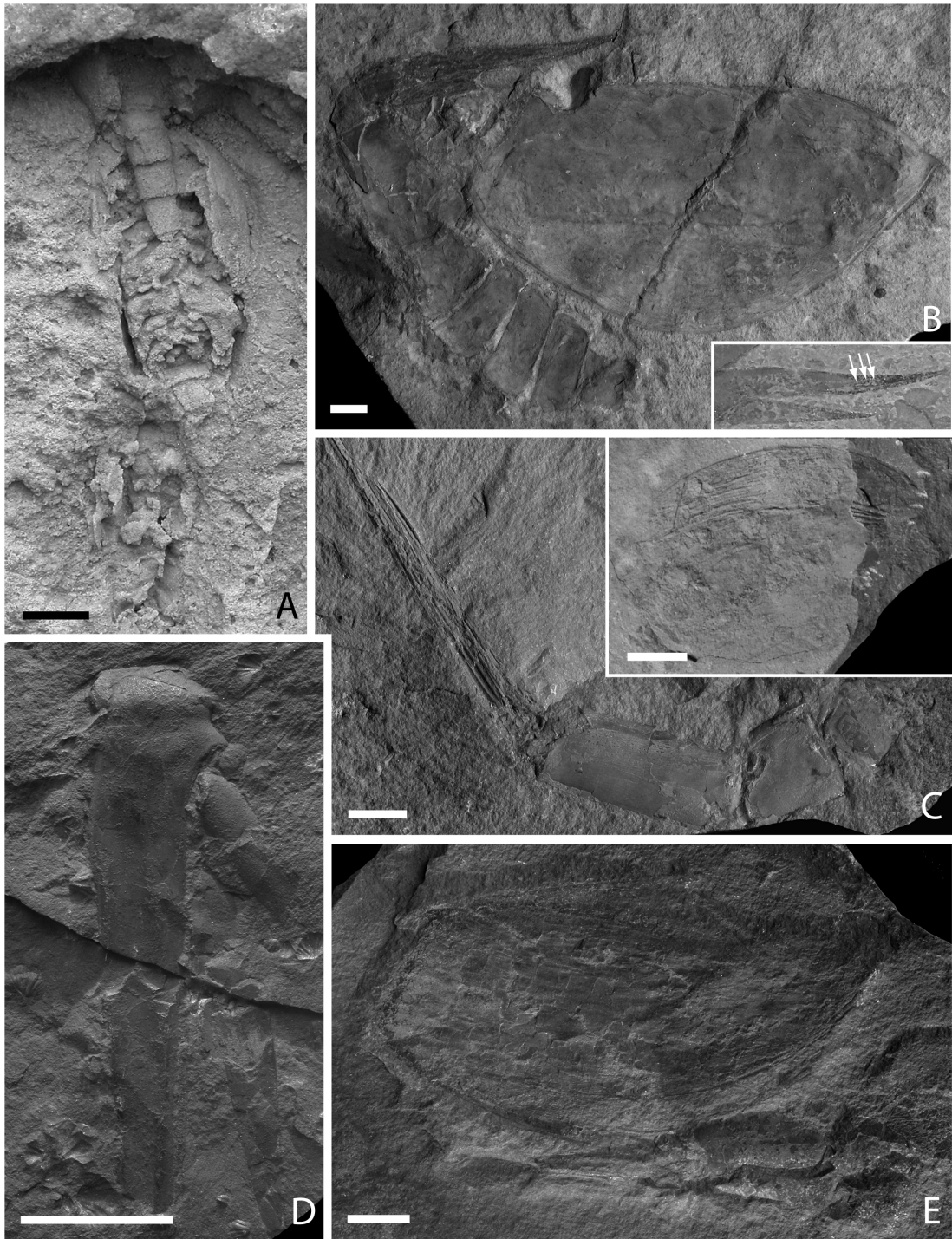


Figure 14. Members of the genus *Ceratiocaris*. A – *Ceratiocaris maccoyanus*, P-665,. B – *C. praecedens*, NYSM 4179, a nearly complete left carapace valve. C – *C. pusilla*, ROM 460-S, syntype, showing anterior carapace margin, articulated greatly elongate telson, and anterior rostral plate. The small size of the specimen precluded photography of the fine longitudinal striations (not visible). Photo courtesy of D. Rudkin. D – *C. pusilla*, HMCZ 6017, showing isolated abdomina/telson assemblages. Note the preferred orientation of the telsons. E – *C. telleri*, NMNH un-numbered example showing a largely complete rare phyllocarid. F – *C. telleri*, NMNH un-numbered example, showing the morphology of the dorsal surface of the telson. G – *C. silurica*, NMNH 66182. Note the elongate carapace and sinuous posterior margin. Scale bars A – F = 1 cm; G = 5 mm.

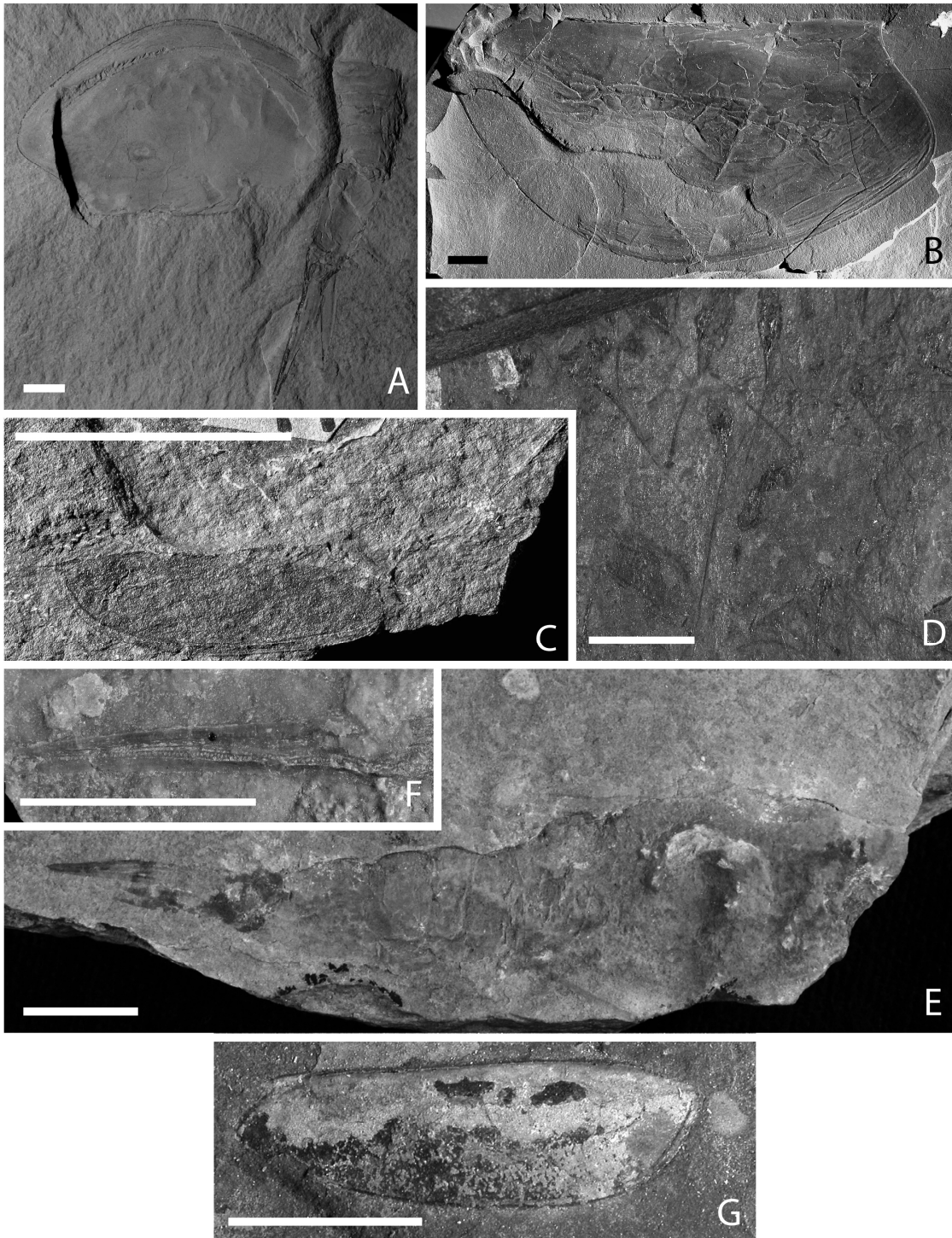


Figure 15. Members of the genera *Pumilocaris*, *Emmelezoe*, and *Caryocaris*. A – *Pumilocaris salina*, NYSM 9678, showing two individuals. The top example is articulated, and shows the telson extending beyond the posterior carapace margin at left. B – *Caryocaris curvilata*, NMNH 81631, a complete left carapace valve. C – isolated telson and furcal rami attributable to *C. curvilata*, NMNH 81631. D - *C. stewarti*, NMNH 139854, showing both dorsal and ventral convex margins and anterior rostral process continuing anteroventrally at approximately the same angle as the anterodorsal margin. E – *C. subula*, ICh 561a, complete, well-preserved right valve showing morphology. F – isolated telson and furcal rami attributable to *C. subula*, ICh 741. G – *C. wrighti* ICh 587a, complete very well-preserved right carapace valve. H - Telson and furcal rami directly associated with *C. wrighti*, ICh 571b. I – *Emmelezoe decora*, NYSM 4430, complete left valve showing the character of the anastomosing carapace ornament. J – *E. decora*, NYSM 4434, nearly complete abdomen, showing the detail of the abdominal ornamentation. Note the scale in both figures 15I and 15J. The abdomen in this species was greatly elongated, protruding a long distance beyond the rather short carapace valves. All scale bars = 1 cm.

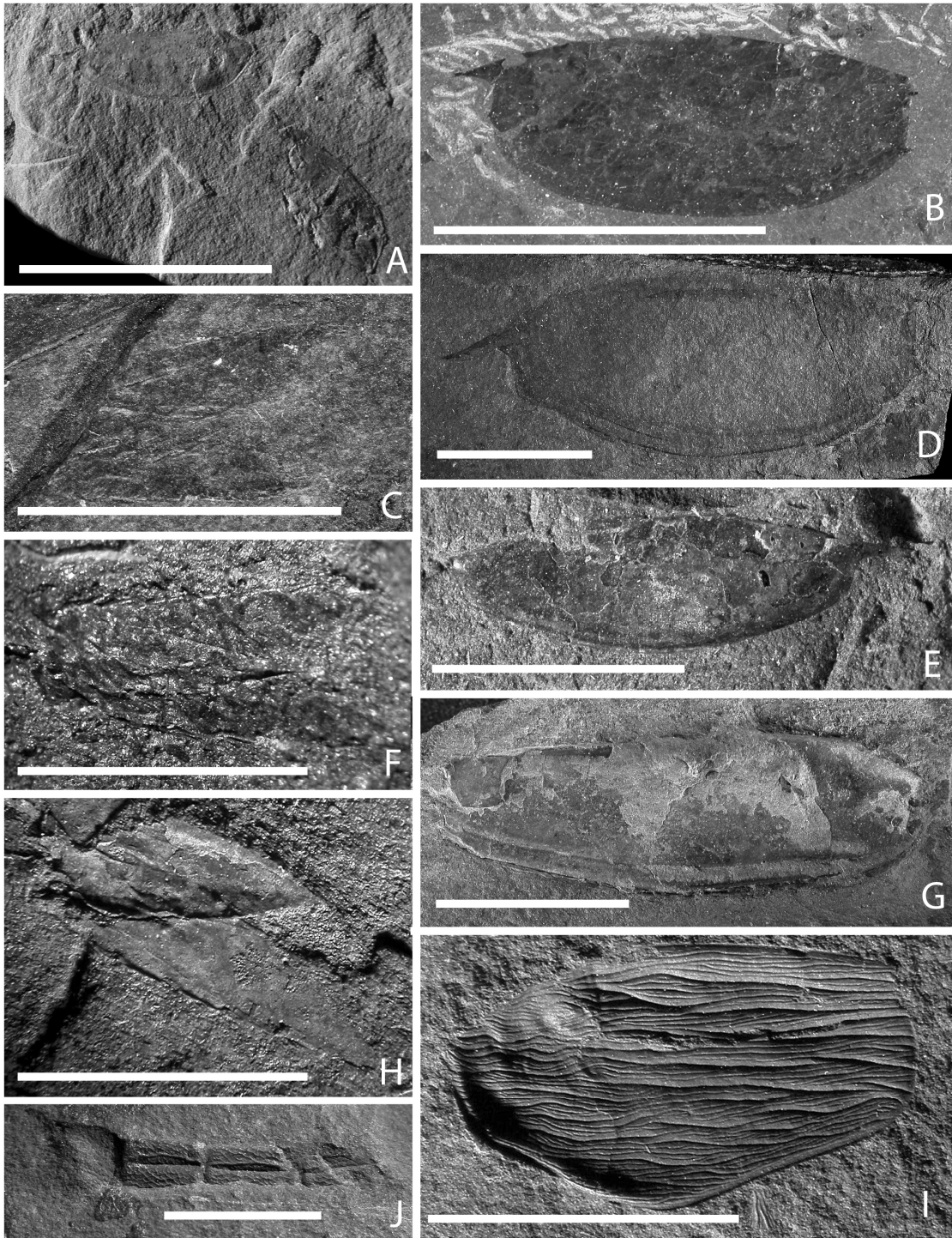
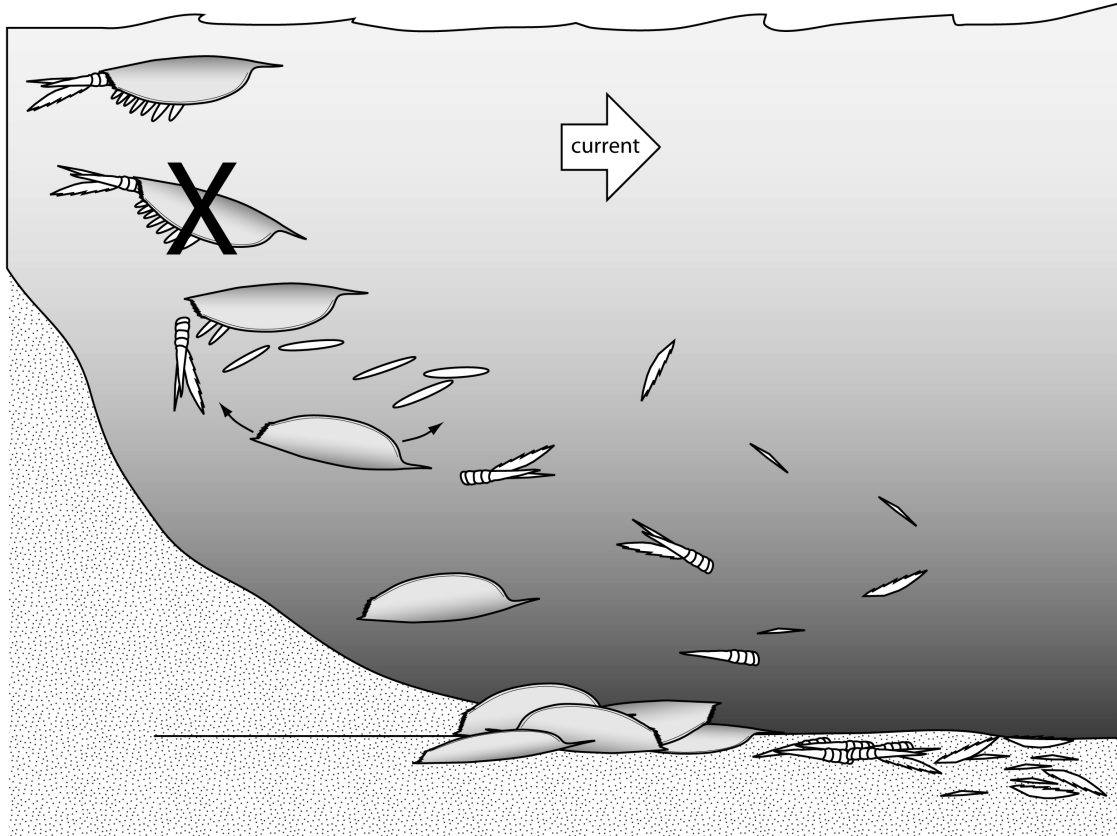


Figure 16. Hypothesized planktonic life habit of caryocaridids. Diagrammatic representation of hypothesized planktonic life habit of caryocaridids, showing death, disarticulation, and stylized preferential sorting due to differential settling and current flow velocity.



CHAPTER 3.

DEAD IN THEIR TRACKS: CAMBRIAN ARTHROPODS AND THEIR TRACES FROM INTERTIDAL SANDSTONES OF QUEBEC AND WISCONSIN.

Introduction

Unequivocal links between trace fossils and their specific producers are exceptionally rare in the fossil record (Caster, 1940; Osgood, 1970; Pickerill and Forbes, 1978; Mikuláš, 1990; Seilacher and Fortey, 1997). This disparity is due to difference in conditions required for the preservation of trace and tracemaker, and to the fact that carcasses are transportable, but trackways generally are not. Coarser clastics that facilitate preservation of trace fossils tend to destroy body fossils; conversely, many fine-grained shales that facilitate soft-tissue preservation represent low oxygen conditions where very few bioturbating animals live. Yet trace fossil linkages are important because trace fossils provide ecological (environmental and ethological) information about soft-bodied animals that are not usually preserved (Osgood, 1975); and because they elucidate how and why body parts on extinct animals were used. In siliciclastic strata, conditions that favor trace fossil preservation include: presence of biofilms, a difference in sedimentological makeup of vertically adjacent beds (sand over mud), shallow subsurface beds with different sedimentology than those above them (allowing undertrack preservation), or lined burrow systems (Bottjer et al., 2000; Jensen et al., 2005; Seilacher 2007, 2008).

There are two categories of trace fossil associations, close associations and mortichnia. Close associations are where a trackway is linked with a particular

organism, but where an animal is not preserved at the end of or in/atop its trace. In these cases, trace and potential maker are both of similar size, co-occur in the same paleogeographic area (often on the same bedding planes), and are morphologically compatible (Hesselbo, 1988; Fortey and Seilacher 1997).

Mortichnia are associations where an animal died atop, in, or at the end of its trace fossil. Rare, notable examples include the 'horseshoe crabs' *Mesolimulus walchii* preserved at the ends of their trackways (Caster, 1940; Malz, 1964; Barthel, 1990), the polychaete annelid *Trentonia shegiriana* preserved at the end of its trail (Pickerill and Forbes, 1978), and the ophiuroid *Taeniaster bohemicus* preserved within its cubichnion, *Asteriacites lumbricalis* (Mikuláš, 1990). In the case of Solnhofen, even the cause of death is known; turbidity currents periodically delivered live animals into the anoxic bottom waters where they would rapidly expire due to lack of oxygen (Seilacher 2007).

Late Cambrian shallow wave- and tide-influenced facies of Laurentia contain a rich trace fossil record (Summerson 1951; MacNaughton et al., 2002; Dix 2004; Hoxie and Hagadorn, 2005; Hagadorn 2008; Getty and Hagadorn, 2008), and rarely, arthropod body fossils (Nelson 1951; Wahlman and Caster, 1978; Hesselbo 1992; Collette and Hagadorn, 2008).

A suite of new Cambrian trace-body fossil associations is described from both the Elk Mound Group of Wisconsin and the Potsdam Group of Quebec which allow linking these records together. Trace fossils include resting, locomotive and mortichnial furrows which are directly associated with large phyllocarid and euthycarcinoid-like arthropods *Arenocaris inflata*, *Mosineia macnaughtoni*, and *Mictomerus melochevillensis*. Closely associated traces are also described and

interpreted; these include “muddled traces” which record movement of arthropods at and below the sediment surface, and across a range of tidal microenvironments.

These associations clarify our understanding of early phyllocarid behavior and how it relates to extant leptostracans, and may link *Mosineia macnaughtoni* and *Mictomerus melochevillensis* to subaerially- and subaqueously-produced *Protichnites*.

Four different types (I – IV, below) of these trace fossil associations are documented from the Blackberry Hill Lagerstätte (Elk Mound Group, Wisconsin) and Potsdam Lagerstätte (Potsdam Group, New York, Quebec, and Ontario). Both the Elk Mound and Potsdam Groups are epicratonic sheet sandstones, deposited along the margins of Laurentia as it straddled the equator in Late Cambrian (Furongian) time. All of the trace fossils described here were produced in shallow to emergent intertidal environments (Hagadorn et al., 2002; MacNaughton et al., 2002; MacNaughton et al., 2003) and occur in fine- to medium-grained, well-sorted, sub-angular to sub-rounded mature quartz arenites and orthoquartzites (Driese 1981; Byers and Dott, 1995; Aswasereelert et al., 2008; Hagadorn and Belt, 2008). Specimens and silicone peels of large uncollectable bedding surfaces described here are repositied in the collections of the Paleontological Research Institution (PRI) and the Royal Ontario Museum (ROM).

Phyllocarid Traces

Phyllocarid crustaceans (*A. inflata*) are known from more than forty specimens in the Elk Mound Group, and are preserved as either three-dimensional casts of the ventral surface, or flattened complete to partially disarticulated impressions (Collette et al., In Review). Three-dimensional casts are interpreted as representing *in situ* animals

that were attempting to escape interment in the overbank mud of a tidal channel when they expired, and flattened incomplete examples possibly represent exuviae (see below). Phyllocarids are preserved on and near a channel levee (Fig. 1A). Their close association with a channel allows for the possibility that they might have ventured out of the channel during times of high water to move about in the overbank mud deposits that were laterally adjacent.

Two types of trace fossils are associated with phyllocarids. The first is a type of *Rusophycus* described below (II) which occurs in the overbank muds and which indicates that the animals burrowed into the underlying mud. The second type of trace fossil are trackways that are terminated by *Arenocaris inflata*, including one sole characterized by an arcuate raised surface burrow that terminates in a three-dimensionally preserved phyllocarid body fossil. Along its length, there are fan-shaped markings at turns that are consistent with impressions made by the repeated outswinging of a tail as the animal turned. This specimen is preserved in both concave and convex hyporelief, and has appendage scratches oriented perpendicular to the axis of the trace (Fig. 1E). This 27.8 cm long surface trail is relatively shallow, and in its final 11.3 cm, the burrow gradually becomes deeper (concave hyporelief) and individual limb impressions become resolved (Fig. 1E). This unusual *Cruziana*-like trackway is comparable to other mortichnia, particularly crustacean and limulid forms from the Solnhofen, in which animals are transported into anoxic bottom waters and meander briefly before death (Caster, 1940; Seilacher, 2007). This trackway was probably produced in a warm, shallow, ephemeral pool that may also have been anoxic.

Probable Phyllocarid Traces

Well-preserved *Rusophycus* co-occur with *A. inflata*, and are preserved in concave hyporelief on bed soles (Figures 1C, 1D). These *Rusophycus* are small (2.2–3.5 cm long, 1.8–2.7 cm wide), bilobate excavations with a sharply defined longitudinal medial crest. Lobes are convex in cross-section, increasing in convexity laterally until vertical; in longitudinal section the lobes are slightly convex from the posterior edge to approximately the midpoint, with convexity increasing markedly toward the anterior. The outline of these rusophycids is oval, with the posterior edge often truncated; the greatest width occurs approximately at the midline. Limb impressions and scratches have not been observed.

The observed size range of these traces correlates very well with the range of sizes measured from *A. inflata*; additionally, both *A. inflata* and these *Rusophycus* co-occur on the same bed soles. Elsewhere, the same *Rusophycus* also occur at the terminations of fan-shaped furrows like Fig. 1E. According to criteria outlined in Fortey and Seilacher [(1997) and enumerated above in the introduction)], the association between *A. inflata* and these rusophycid traces is well-supported, strongly suggesting a phyllocarid origin.

Possible Phyllocarid Traces: “Muddled Burrows”

Two types of traces in these strata are ‘muddled’; that is, they represent pulse-like or stop-and-start behavior, consisting of a series of repeating, oval rusophycid-like shallow burrows that often display scratches or limb impressions that vary widely in their orientations. One of these traces (described here) represents infaunal, and the

other represents epifaunal furrowing and trackmaking (IIIB, below). The ‘muddled burrow’ provides a potential linkage between *A. inflata*-like arthropods and infaunal and epifaunal behaviors (see ‘Muddled Surface Trails’ below) (Fig. 2A–2C). The ‘muddled burrow’ (Figs. 2A–2C) is a bilobate, approximately circular burrow 64.3 cm long. It is preserved in convex hyporelief, and co-occurs with *A. inflata* body fossils in the Elk Mound Group. In cross-section, this burrow is W-shaped; the two lateral walls are fairly deep (up to 5 mm) and are approximately perpendicular to horizontal. The medial part of the trace is relatively wide (to 1 cm), and slightly concave (Figs. 2A–2C). Scratches or limb impressions are present extending from the midline of the burrow outward at varying orientations, giving the impression of ‘muddled burrows’; these appendage marks often extend past the clear lateral margins of the burrow (arrowed ‘s’, Fig. 2C). A number of Y-shaped impressions are distributed over the course of this surface burrow, with the distal, pointed end of the Y always oriented pointing clockwise (arrowed, Fig. 2A, 2B). The outline of the burrow appears to regularly shrink and swell (outlined, Fig. 2A), giving the trace a rope-like appearance in outline.

These ‘muddled burrows’ are interpreted as fodichnial structures of phyllocarids because they co-occur with *A. inflata* on the same slabs. These burrows co-occur with phyllocarid fossils on the same bedding planes (often less than a centimeter from one another). Carapaces of *A. inflata* are consistently similar in width to these muddled burrows which themselves vary little in width. Additionally, peristaltic, rusophycid-like impressions are similar in size and shape with carapaces of *A. inflata*. Modern leptostracans do not manipulate sediment at the surface in this manner, but deposit-feed

infaunally (Cannon, 1927; Martin et al., 1996). Other burrows interpreted as having been phyllocarid-produced also possess a rusophycoid element (Hannibal and Feldmann, 1983). The rope-like appearance of this trace is interpreted to have been caused by the intermittent forward motion of *A. inflata* through the sediment, producing a continuous series of overlapping rusophycoform structures as it manipulated the sediment; these rusophycoform ‘burrow segments’ correlate very well to measured widths of *A. inflata* present on the same bed sole. The depressed medial portion of this surface burrow (topography is reversed due to this being a bed sole) represents the originally positive mound of sediment drawn inward from the lateral margins of the burrow as the animal processed the mud. They are similar in width to the posterior portion of *Rusophycus* described in II above. The bifurcate medial furrows present are interpreted as representing the margins of the carapace. As sediment was drawn inward by the appendages, the posterior margins of the carapace would drop below the sediment/air or sediment/water interface. The continued burrowing activity combined with the pulse-like forward motion of the animal as it moved forward to unprocessed sediment produced the bifurcate medial furrows seen in this example. The Y-shaped, posteriorly directed impressions are interpreted as the impression of an abdomen, telson, and/or furcal rami (Fig. 2B, arrowed). Because no telson has been found preserved with *Arenocaris inflata*, the morphological details of this structure remain unknown. As the animal propelled itself forward for successive sediment processing, the convex hyporelief appendage marks were produced in succession.

In the modern leptostracan phyllocarid *Nebalia bipes*, feeding is infaunal, and occurs in mud (Cannon 1927; Martin et al., 1996). The rostral plate, an articulated

process at the anterodorsal junction of the carapace valves, controls the flow of material into the filter chamber (ventral portion of the pre-abdomen, including thoracopods (thoracic appendages), head appendages, and the ventral valve surfaces) (Cannon, 1927). The thoracopods have a dense fringe of setae along the inner edge of the endopodite (inner branch of biramous thoracopod), and also a dense frond of setae at the distal end of the endopodite; these setae interlock with those of adjacent and opposite limbs creating a filter- or brood chamber (Cannon, 1927). As sediment passes through the filter chamber, small organic particles are collected and passed forward to the mouth (Cannon, 1927; Rowett, 1943). Given the peristaltic, pulse-like motion through the sediment shown in the muddled burrows, it is plausible that the producer of this burrow also employed this method of infaunal feeding.

Only three trace fossils have been attributed to phyllocarids, a fact at odds with the relatively common occurrence of the subclass Phyllocarida throughout the Paleozoic. Un-named trace fossils interpreted to have been fodichnial burrows made by ceratiocaridid phyllocarids occur in the Silurian Eramosa Formation of Ontario (Tetreault, 2001). *Svalbardichnus trilobus* was interpreted as a resting trace from the Lower or Middle Devonian of Spitsbergen, and attributed to a rhinocaridid phyllocarid (Wisshak et al., 2004). It consists of an infaunal trilobate structure much more like a typical *Rusophycus*, but constructed below the sediment at the interface between a conglomerate and the underlying floodplain mud (Wisshak et al., 2004). The shallow surface burrows made by Elk Mound phyllocarids resemble none of the preceding very closely. One trace fossil that has been attributed to a phyllocarid tracemaker is *Chagrinichnites osgoodi* from the Late Devonian of Ohio (Hannibal and Feldmann,

1983). It was interpreted as both an infaunal feeding burrow and escape structure depending on the orientation of the traces (horizontal vs. vertical respectively) of a probable echinocaridid phyllocarid (Hannibal and Feldmann, 1983). It is possible that muddled burrows from the Elk Mound Group represent similar infaunal utilization of the sand/mud interface.

Possible Phyllocarid Traces: Muddled Surface Trails

Abundant ‘muddled surface trails’ also occur atop laterally extensive undulatory bedding planes in the Elk Mound Group. In one example, where the margin of a shallow tide pool is preserved, several behaviors consistent with modern leptostracan behaviors can be documented (Fig. 3A). Three thin but distinct stratigraphic beds are present on this outcrop surface; the lowest (~10% exposure) is a 3 cm thick bed dominated by sinuous crested, asymmetric ripples trending toward 280° (Fig. 3B labelled ‘L’). No microbially-produced structures are present on the surface of this lower bed. The middle bed [~20% exposure (Fig. 3B ‘M’)] is 1.5 cm thick, lacks ripples, and is covered with 3 mm – 3 cm diameter pustular structures and sand stromatolites (Fig. 3B, labeled ‘ss’) interpreted to represent microbial buildups. The uppermost bed (~70% of the exposure) is covered with low amplitude, washed out interference ripples (Fig. 3B ‘U’); deeper portions of the pool lack interference ripples (labeled ‘P’ in Fig. 3A). Each of these individual beds is interpreted as a single, temporally short-lived depositional event.

There are at least sixteen gently curving to arcuate “muddled surface trails” present on the uppermost bed (Fig. 3C labeled ‘st’). Surface trails are preserved in

concave epirelief, range in width from 15.2 mm to 23.9 mm, with lengths of up to 1.15 m. Traces are similar to the muddled burrows, but have reverse relief because they occur on a bed top, not a sole. Thus, the lateral furrows are less deeply impressed in the sediment, and the pulse-like lobes and individual appendage marks are much less pronounced. Individual appendage marks are also less well preserved. These differences in morphology may result from mud having been present in the underlying layer in the muddled burrow slab, thus preserving the trace with much more detail. In contrast, the muddled surface trails were constructed epifaunally over sand.

Muddled surface trails were constructed at the sediment/water interface, which may not have been the case with the looping, circular muddled burrow. The presence of an underlying mud layer without desiccation cracks in looping muddled burrows suggests a subaqueous origin; whereas topography and sedimentary structures suggest a subaerial origin for the muddled surface trails. In all examples present on the surface represented in Fig. 3A, surface trails emerge from infaunal burrows (Fig. 3C labeled 'i'), and grade into epifaunal surface trails (labeled 'st' Fig. 3C). Although the soles of these burrows were not visible, and could not be spalled from the rock surface, they are consistent in size, shape, and appearance with the dorsal portion of burrows described in IIIA. The transition from infaunal to epifaunal is shown by the dramatic difference in morphology of burrows (round to elliptical in outline, upward angle, differing color of burrow fill) compared with surface trails (traces abruptly emerge onto this surface from underlying levels, follow local topography, cross-cut one another, and shallow as they enter standing water). After continuing in an arcuate path, the surface trails gradually become very shallow (Fig. 3C 'sh') and terminate in a series of carapace

‘touch-down’ traces in the topographically lowest part of the surface (Fig. 3D ‘td’).

Figure 3D illustrates an infaunal burrow originating from the middle, microbial structure dominated bed, moving to the upper washed-out ripple dominated surface, and terminating in a carapace touch-down trace (Fig. 3D inset shows the two terminal touch-down traces associated with this trackway).

Infaunal burrows are generally slightly darker in color than the surrounding matrix, and as individual burrows transition from infaunal to surface trails, they increase in width. This change in width is consistent with an arthropod which possesses a bivalved carapace. Because such carapace valves are typically convex when viewed from above, forming a lozenge- or ellipse-shaped carapace, forward motion through sediment would act to compress the valves inward slightly. Such a condition would not persist once the carapace was not constrained by sediment, and the valves could slightly expand. The morphology of the infaunal burrows is similar to the muddled surface trails as well as the muddled burrows, suggesting that the method of construction/ambulation was similar whether the tracemakers were travelling over the sediment or through it. In the muddled burrows, the deeper lateral furrows and slightly greater height of the medial part of the trackway is suggestive of inward manipulation of sediment, and may represent furrowing, sediment processing, or feeding structures. In the infaunal burrows associated with these muddled surface trails, not enough detail is preserved to assess whether these were feeding structures (fodichnia) or simply represent traces generated by locomotory activity within the sediment (repichnia). However, the abundance of buried microbially-produced structures represents an abundant potential food source. Where infaunal traces are visible in the two lower

beds, the traces follow bed interfaces, which would be consistent with a subsurface feeding strategy.

There is also the possibility that tracemakers stranded during ebb tide may have burrowed as an anti-desiccation mechanism. Many modern leptostracan phyllocarid species burrow as a means of hiding, resting, or as a feeding strategy (Cannon, 1927; Vannier et al., 1997). In leptostracans that inhabit the intertidal zone, strategies for resisting desiccation at low tide vary from resting directly on the sediment surface under mats of algae (Haney and Martin 2000, 2005), or resting shallowly buried in the sediments (Vannier et al., 1997). Multiple tracemakers on the surface in Fig. 3A emerged from underlying levels, moved on the surface of the sediment toward the topographically lowest part of the surface, and then disappeared in a series of touch-down traces. Perhaps these traces represent the response of shallowly-buried phyllocarids to the return of high tide, when it was once again safe to emerge from burial and return to the surface.

Euthyucarcinoid-like Traces

In the Potsdam Group of Quebec, the enigmatic arthropod *Micromerus melochevillensis* (Fig. 4B) occurs at the ends of *Cruziana*-like trace fossils on polygonally cracked surfaces (Figs. 4A and inset, 4C–E). Potsdam cruzianid traces are preserved in convex hyporelief on bed soles. One example, a large (2.24 m long x 1.22 m wide x 71 cm deep, Fig. 4A, and inset) slab of fine to medium grained, sub-angular to sub-rounded, planar to low angle cross-bedded quartz arenite contains many smooth, slightly curved to sinuous surface trails of varying length. The traces range in width

from 2.3 to 4.0 cm, with a mean of 3.4 cm ($n = 30$). Exposed length varies from 12.4 to more than 80 cm, but length measurements probably represent a minimum of actual length because parts of the trails were not excavated as deeply and disappear into overlying sediment. Trails commonly cross-cut each other, but do not overlap themselves. The nature of the medial region is uncertain, because subsequent post-mortem cracking of the underlying mud has longitudinally bisected nearly all of the specimens. The best preserved trails are flanked by sloping convex lateral bevels (labeled 'b' Fig. 4D), like those described by Young (1972). These bevels are delimited by deep, well-defined outer marginal grooves.

Despite the obliteration of the medial structure of these trackways, some faint morphological details are visible on two specimens - ROM 59386 (Fig. 4B) and CR-13 (Fig. 4D). In CR-13 (Fig. 4D), morphological features closely resemble the ichnogenus *Didymaulichnus*. Similarities include faintly preserved bilobate structure (labeled 'l' Fig. 4D, see also cross-section, Fig. 4B), a median furrow (in this case relatively open and wide), and deep parallel lateral grooves ('g' Fig. 4D). On the original epichnial surface, these grooves would have been ridges, generated by sediments being pushed forward and laterally as the arthropod pushed its way through the mud.

Overall, ichnotaxonomic assignment is problematic. The bilobed furrow is common to both *Cruziana* and *Didymaulichnus*, but the traces lack striated ornamentation to differentiate between the two. Absence of within-trace details may result from several factors. It is possible that the mud was still saturated with water when the traces were constructed, or that fine details have been washed out by subsequent erosion, or loading from overlying sand.

Taphonomic Model of Arthropod Body Fossils

It has been suggested by recent authors that exceptional preservation of trace fossils in the Cambrian was mediated by the presence of microbial mats (Hagadorn, 2008; Seilacher 2008). However, the onset of the Cambrian substrate revolution, in which a dramatic increase in bioturbation and utilization of microbial mats as a food source, made it difficult for mats to become established (Seilacher and Pflüger, 1994; Seilacher 2008). Microbial structures (e.g., old elephant skin, sand stromatolites, oscillation ripples with hollowed-out crests, and pustular surface textures) and trace fossils present on Elk Mound sand flats indicate that the Cambrian substrate revolution had not yet made it into the intertidal zone of Laurentia by the Furongian (Seilacher, 2008). Additionally, microbial textures associated with many scyphomedusae fossils from the Blackberry Hill Lagerstätte indicate that preservation of soft tissues in Cambrian intertidal facies may have been microbially mediated (Tarhan and Hagadorn, 2008). Three-dimensionally preserved arthropod fossils from Wisconsin, however, do not show evidence of microbial mediation in preservation.

Three-dimensional preservation of body fossils in sandstone is not unique in the fossil record. The Ediacaran Fauna is preserved in convex hyporelief on arenitic bed soles and in sandstone (Narbonne 1998; Grazhdankin 2004). In the Phanerozoic, however, this style of preservation becomes much less common. In addition to the phyllocarid, mosiniensid, and mictomerid arthropods from the Furongian of Wisconsin and the Quebec (Collette and Hagadorn, 2008), few other occurrences have been documented. A slab of chasmataspid-like arthropods from the Upper Cambrian (Dresbachian) Hickory Sandstone of Texas are preserved as casts of the ventral surface

of the animals (Wahlman and Caster 1978; Dunlop et al., 2004). A single euthycarcinoid arthropod from the Silurian Tumblagooda Sandstone of Western Australia is preserved as a ventral cast in medium- to coarse-grained quartz sandstone (McNamara and Trewin, 1993).

Ediacaran organisms lived on a sand or mud substrate which was often microbially bound, and in mud settings like the Ust-Pinega Formation (i.e., White Sea Biota) were impressed into the underlying mud by the rapid deposition of storm sands (Narbonne 1998; Gehling 1999; Grazhdankin 2004). Three-dimensionally preserved arthropod body fossils from Quebec and Wisconsin share key characteristics with White Sea-type Ediacaran preservation: they both required a mud substrate to form a mold of the organisms, and they were both cast in sand. However, Quebec and Wisconsin arthropods are preserved in much more robust, three-dimensional relief with very little compaction.

Arthropod fossils from Quebec and Wisconsin are preserved in convex hyporelief on bed soles (Figs. 1A, 1B; 4A, 4B). A complete lack of dorsal preservation indicates that the arthropods are preserved in life position. Three-dimensional arthropod body fossils always occur on soles concurrent with green glauconitic clay veneers, which in turn are often associated with discrete channels. These clay horizons represent overbank deposits of shallow channels, and are often associated with large-scale (up to 2 cm wide) subaerial polygonal desiccation cracks. Cracks have T-shaped intersections and casts of inter-crack areas indicate mud clasts had upwardly curled edges. Because these mud cracks never cross-cut the arthropod fossils, intact arthropod remains must have been present prior to crack formation. A hypothetical taphonomic

model that explains all of the observed primary sedimentary structures is given in Figure 5. This model, illustrated with phyllocarids, invokes production of three-dimensional hardened mud molds of the ventral surface of arthropods and infilling of these molds with sand.

The first step of this model involves stranding of arthropods by high water. Stranding might result from a spring tide, a storm surge, or an end-monsoonal cycle, and would allow arthropods that had been confined to a channel to access overbank mud. Because *Rusophycus* co-occur on bed soles, these overbank mud deposits might have represented a desirable food source.

As the water receded, the arthropods became trapped in the overbank muds. Locally, ephemeral pools were probably present. Support for the presence of these pools is given by the distribution of arthropod remains in Figures 1A and 4A, in which clustering occurs in areas representing topographic lows where water would have been deeper. Other areas of large arthropod-bearing bed soles lack desiccation cracks and have been loaded by sand, indicating that the mud in these areas was still pliable when sand deposition took place. During this interval, it is possible that the arthropods burrowed into the unconsolidated mud to avoid desiccation. This would have allowed clay minerals to coat the ventral surfaces, preserving limb detail in three-dimensions. The overbank ephemeral pool then desiccated, encasing the lower portions of the arthropods in hardened clay (Fig. 5C). Polygonal desiccation cracks do not cross-cut arthropod fossils, thus arthropod remains must still have been present to prevent crack propagation. High water again inundates the levee overbank (Fig 5D). A fresh layer of sand is then deposited over the partially decomposed, but probably still intact,

arthropod remains. Because the arthropod remains are now below the surface of the sand, and thus perpetually moist, enhanced bacterial degradation probably decomposes the remains quickly. As degradation ensues, the overlying well-rounded sand gradually moves downward into interstices where the arthropod body was. Because well-rounded sand has a low angle of internal friction, individual grains could cast every cavity in the mold that they could fit into, producing three-dimensional fossils with remarkable detail. Much later, dissolved silica lithifies the sediments and the arthropods were preserved (Selleck, 1993).

Interestingly, the clay that mediated preservation of the fossils is still present in an unlithified state; it consists of very fine pale pistachio-green glauconitic clay. It is hypothesized that this clay was lithified to shale at some point in the past, but that groundwater moving through the subsurface broke the shale back down to clay. Three large samples (> 1kg each) of this clay were collected during subsequent field seasons for palynologic and conodont analysis; none were identified.

Implications

New and continuing discoveries in siliciclastic epicratonic sheet sandstones continue to add important details to our knowledge of arthropod morphology and behavior in intermittently emergent Cambrian intertidal settings. In the past, these localities and formations have been thought of as either unfavorable to preservation of soft-bodied or lightly mineralized fossils, or as places where all the interesting work had already been done. The paucity of body fossils in these transitional environments is likely due to a number of factors, including the time transgressive nature of the

marine/terrestrial interface, the relatively high energy of this environment, high oxygen concentration, and daily tidal cyclicity. Recent fieldwork in the Blackberry Hill Lagerstätte (Furongian, Elk Mound Group) of Wisconsin has uncovered not only three-dimensionally preserved soft-bodied arthropods, but a number of new trace fossils that add to our knowledge of the ecology of the paleoenvironment and ethology of the tracemakers. Both the phyllocarid and the *Mictomerus* furrows allow the rare and unquestionable attribution of specific producers to corresponding traces and contribute to our understanding of early arthropod behavior in shallow marine to emergent environments, where animals were first venturing out of the ocean. The association of partially burrowed trails with subaerial desiccation cracks illustrates an adaptive strategy among two groups of early arthropods to cope with harsh conditions occurring on Laurentian tidal flats.

Experimental work is ongoing that will attempt to quantify the hypothetical model presented herein through the production of similar three-dimensional sand-cast arthropod ‘fossils’. This model predicts that the key factor in mediating this style of preservation is the presence of mud or clay. Early results of these taphonomic experiments indicate that arthropod remains interrupted the propagation of desiccation cracks. This indicates that a resistant mold of hardened clay would have formed around the ventral surface of the arthropods, allowing subsequent casting in sand. This new style of Phanerozoic Lagerstätte has currently been documented in three localities: the Furongian Blackberry Hill Lagerstätte of central Wisconsin, the Late Cambrian Potsdam Lagerstätte of southern Quebec, and chasmataspids from the Upper Cambrian Hickory Sandstone of Texas. An additional possible occurrence of this preservational

style may be the Silurian Tumblagooda Sandstone of Western Australia, where a single euthycarcinoid arthropod was found preserved in a similar manner.

A narrow taphonomic window exists in these Late Cambrian sheet sandstones to better understand a key evolutionary interval that lead to early arthropod terrestrialization. Future work will focus on linking the large arthropods *Mosineia macnaughtoni* and *Mictomerus melochevillensis* to *Protichnites* and *Diplichnites* trackways from the Elk Mound and Potsdam Groups. Information on the mechanical properties of gait, stride length, and track depth can give approximations of how fast an animal could move (Braddy, 1997) and allow us to deduce whether it was partially or fully submerged. Known deposits of subaerially-produced (aeolian) protichnitid trackways indicate that limited terrestrialization took place by at least Late Cambrian time (MacNaughton et al., 2002; Hoxie and Hagadorn, 2005; Hagadorn, 2008). Thus, the unusual environmental conditions present in Palaeozoic epicratonic intertidal zones (Rose and Hagadorn, 2006) may have led to development of novel anti-desiccation mechanisms in these large Late Cambrian arthropods.

FIGURE 17— Elk Mound Group traces, producers, and a large slab containing both.

A) Half of a phyllocarid-bearing bed sole from the Blackberry Hill Lagerstätten. Note the prominent channel, the well-defined levee, and the overbank with abundant multi-generation polygonal desiccation cracks. Forty-two arthropod body fossils and five *Rusophycus* were found on this bed sole. Pocket knife is 8.3 cm for scale. B)

Cambrian phyllocarid *Arenocaris inflata* from the Furongian of Wisconsin, Holotype, PRI 10130. C) *Rusophycus* present on PRI 10133. Note the crisp medial longitudinal

crest. Because these *Rusophycus* occur on the same soles as *A. inflata*, and they are similar in size and proportions to the phyllocarid *A. inflata*, they are interpreted to have been constructed by phyllocarids. D) A bed sole showing ten well defined *Rusophycus*.

E) A bed sole preserving at least seven phyllocarids. Note the arcuate trail beginning just above Ar5 and ending at Ar7. Medial scratches are vague, but are present. Well-defined limb impressions (arrowed) are present in the ventrally-preserved phyllocarid at the end of the trace. Scale bars in B – C, E = 1 cm; D = 5 cm.

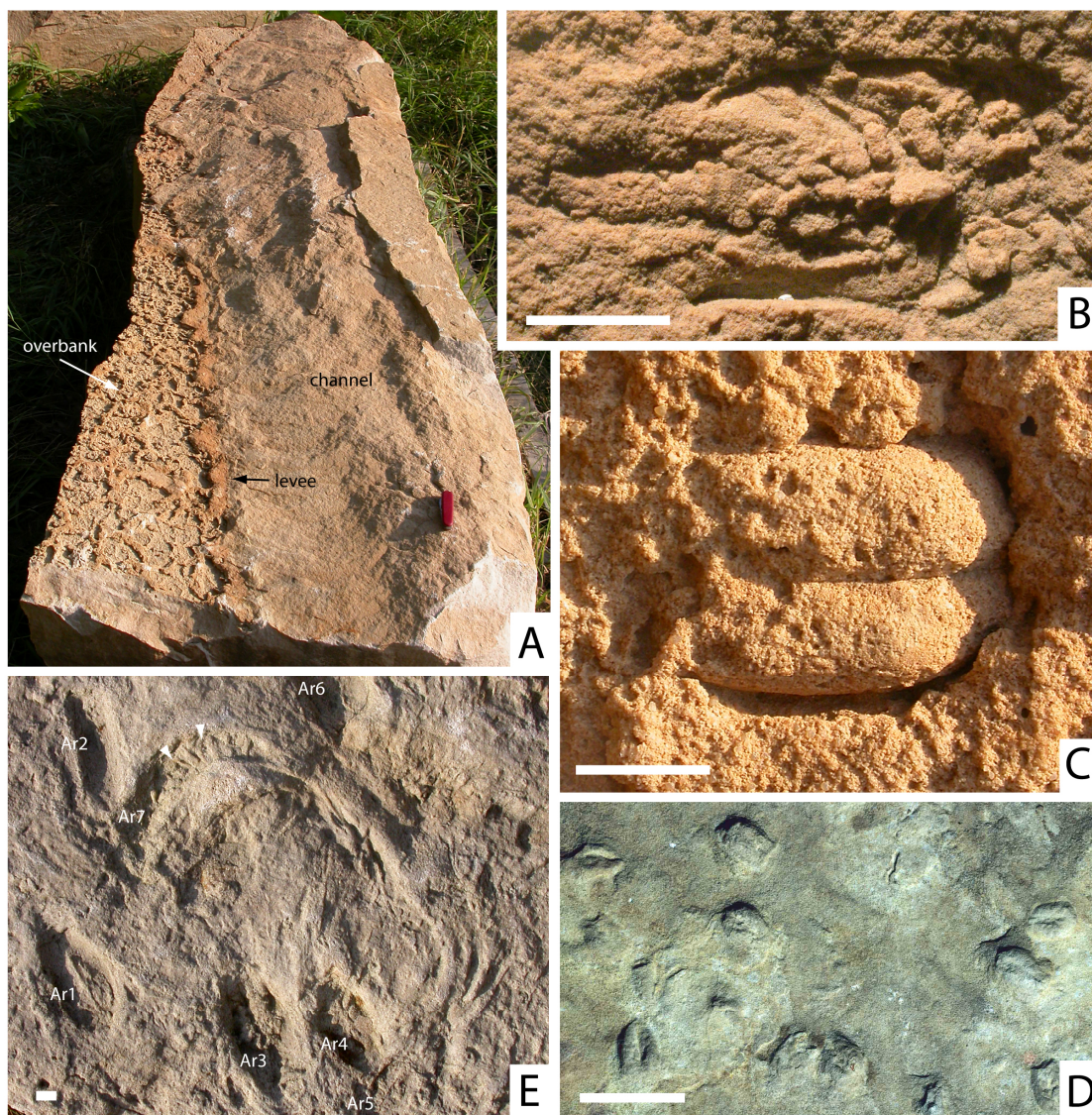


FIGURE 18—Elk Mound Group traces. A) Circular, looping muddled burrow. The trace is deep (≥ 3 mm), has well-defined Y-shaped impressions (arrowed), and has a characteristic ropy, peristaltic outline (outlined in black). B) Close-up photograph of the left side of Fig. 2A. Note the well-defined Y-shaped impressions. C) Close-up of the right side of Fig. 2A. Note the scratches present intermittently along the course of the burrow, the depth of the burrow, and well-defined margins. D) Close up photograph of a muddled surface trail for comparison with Figures 2B and 2D.

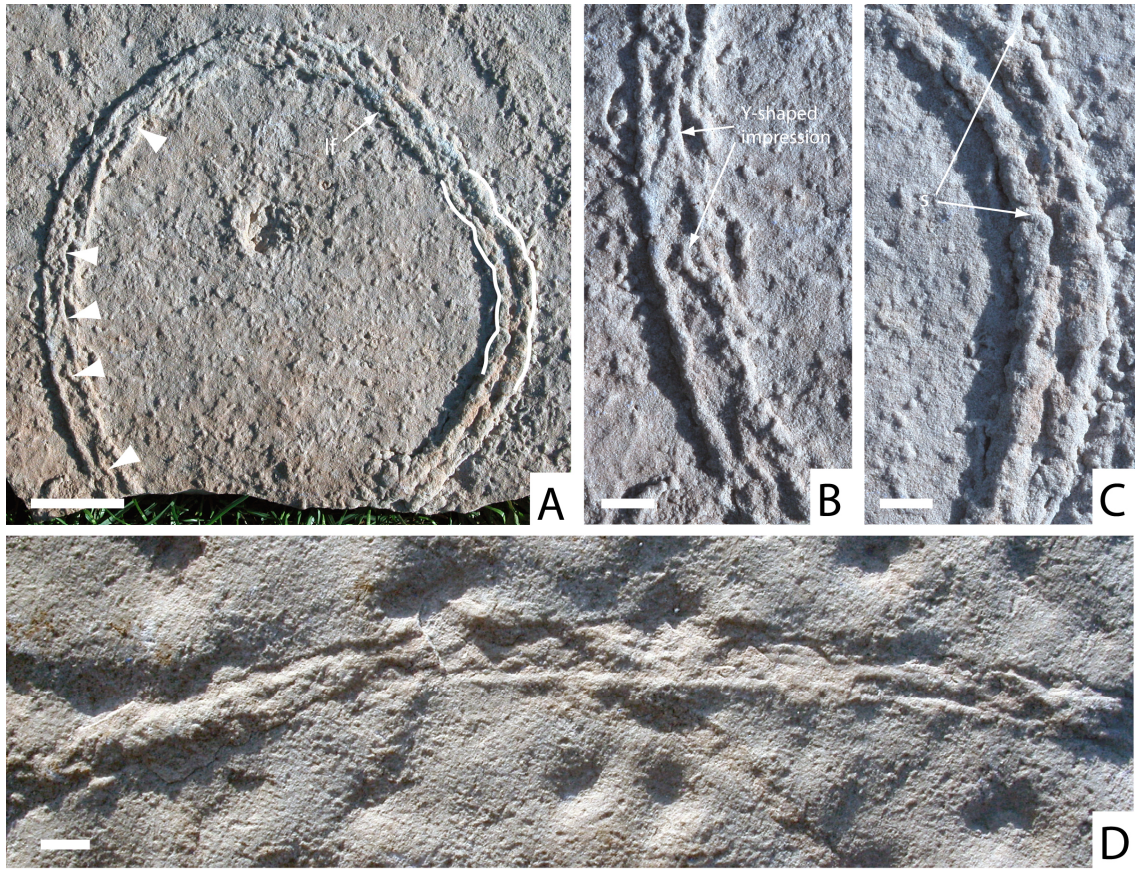


FIGURE 19— EMG traces, representing infaunal, epifaunal, and nektonic activity. A) Map of a large surface (5 by 3 m) showing the exposure of three stratigraphic horizons and their surface features. Note the middle horizon contains abundant microbially-produced structures (sand stromatolites and algal balls). This map shows phyllocarid-produced burrows emerging from underlying beds, moving over the sediment surface, and finally swimming off into the topographically lowest parts of the shallow pool (labeled 'P'). B) Inset photograph showing the three thin beds that make up this surface. Note the abundant small sand stromatolites (labeled 'ss'). U = upper bed, M = middle bed, L = lower bed. C) Arcuate trace fossil from area indicated in box C of Fig. 2A. Note the sudden appearance of the infaunal portion of the trace (labeled 'i'), the gradation into a surface trail ('st'), and the shallowing of the trail at the lower right ('sh'). Note also the deep lateral furrows ('lf'), interpreted as the ventral carapace margin (see also Figure 2D). D) A more linear phyllocarid-produced trace emerging from an underlying bed surface. This trackway begins on the right side as an infaunal burrow paralleling the surface of the algal ball dominated surface, and emerges onto the surface as a "muddled surface trail", and then a series of carapace touch-down traces head off into the topographically lowest portions of the pool (labeled 'td'); thus the direction of the trace was from right to left in this figure. The inset photo shows a close-up of the last two touch-down traces of this trackway. Scale bar in A = 1 m; B and C = 10 cm; D and inset = 3.2 cm.

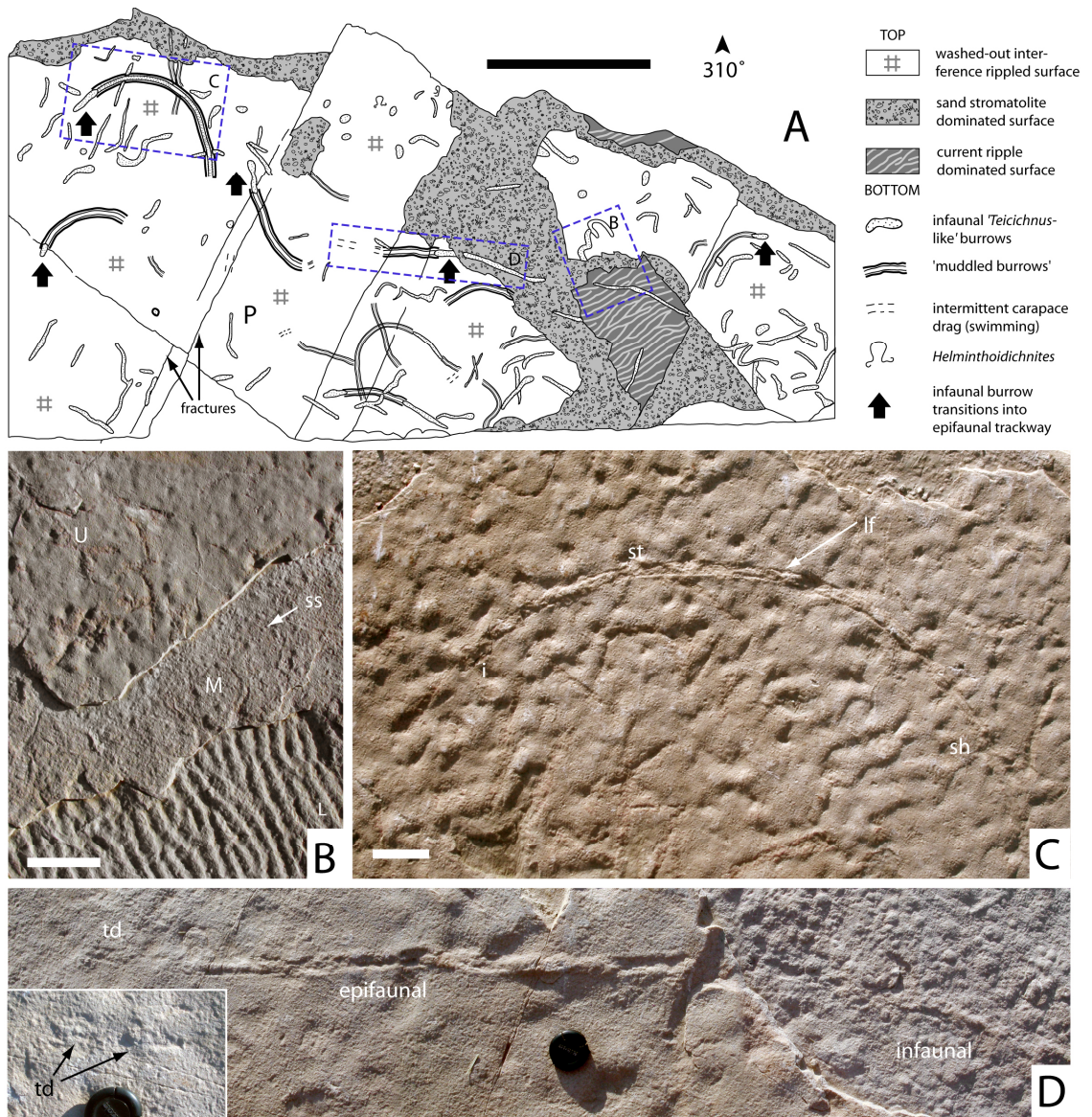


FIGURE 20— Potsdam traces produced by *Mictomerus melochevillensis*. A) Map of a large field specimen (bed sole) and inset photograph of slab, showing distribution of arthropod body fossils (numbered), trackways associated directly with individual body fossils (labeled ‘CR-##a), and trackways not associated with individuals (‘CR-##’). Note that arthropod trackways and mud cracks are often the same shape. B) The holotype of *Mictomerus melochevillensis* (ROM 59386, ventral preservation) showing at least eight homopodous limbs. A bilobate trail with sharply truncated margins leads directly to the posterior of the body fossil. Note bilobate nature of cross-section of trail (a to a’) suggesting that the animal may have been attempting to burrow into the sediment to avoid desiccation. C) Photograph showing the entire bed sole that the holotype of *M. melochevillensis* was found on. D) Cruzianid trackways or burrows produced by *M. melochevillensis*. Note the unusual lateral bevels (‘b’), the lateral grooves (‘g’), and the bilobate structures (‘l’). E) Sub-circular trackway (arrowed), and trackway-mediated mud cracks. Scale bars in A = 1 m; B = 1 cm; C = 10 cm; D – E = 5 cm.

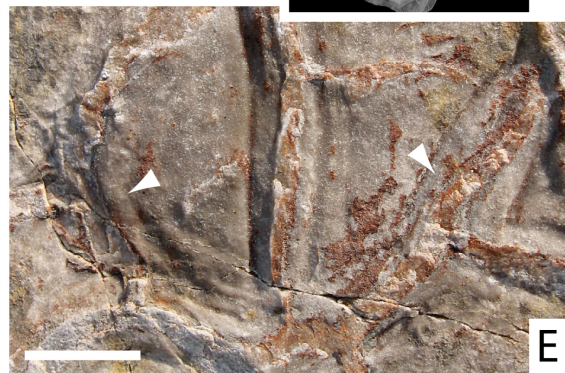
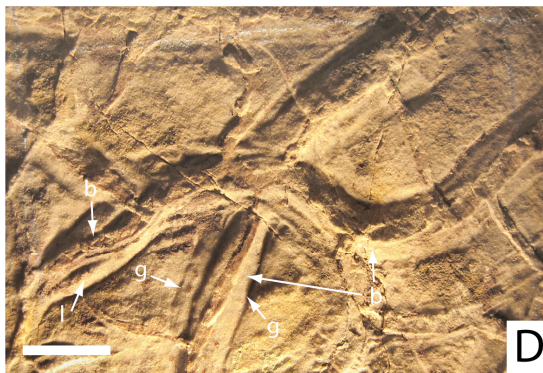
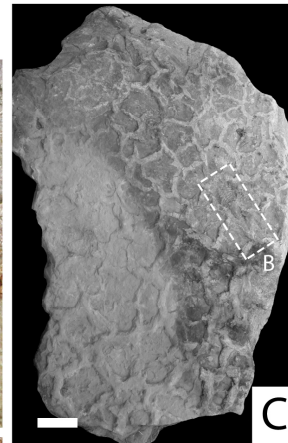
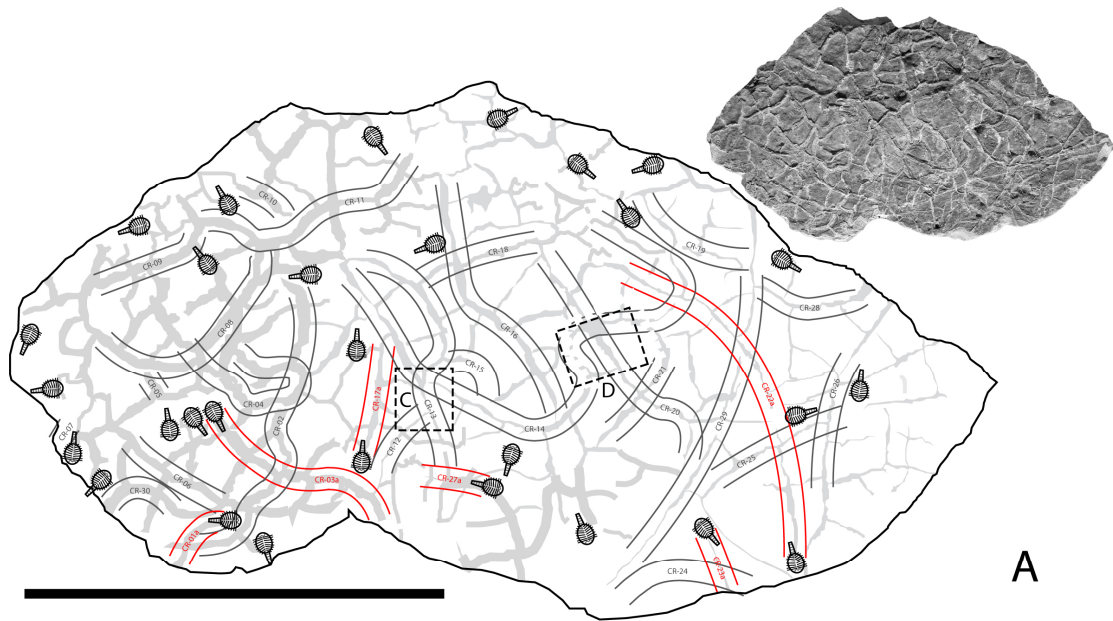
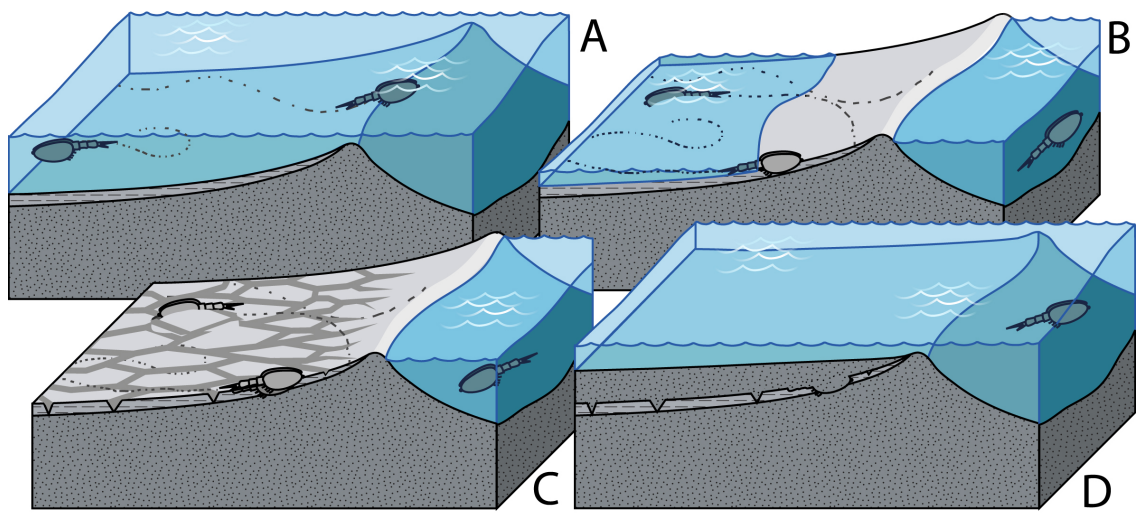


FIGURE 21— Block model explaining the 3-D preservation of arthropods in this study.

Although this model illustration contains phyllocarids, the larger arthropod fossils *Mosineia macnaughtoni* and *Mictomerus melochevillensis* are hypothesized to have been produced in the same manner. A) Seasonally high water allows the arthropods to access overbank areas. *Rusophycus* traces may be produced at this time. B) Water level then drops, stranding arthropods in an ephemeral pool. Individuals may have attempted to burrow into the mud as an anti-desiccation strategy, possibly also producing *Rusophycus* and definitely producing cruzianid- and didymaulichnid-like furrows. C) Water completely evaporates. Large-scale desiccation cracks form, but do not cross-cut arthropod remains, indicating that they remained intact for a time. D) Water level once again overtops the levee, allowing the overbank to flood and sand to be deposited on top of the arthropod-bearing mud. As carcasses degrade, sand drops down into carcass voids, and casts their ventral surfaces and appendages.



APPENDIX I

CHARACTER STATES USED FOR PHYLOGENY

- 1) Anterior horn of carapace: (0) acuminate; (1) rounded; (2) absent.
- 2) Length of carapace horn to body length: (0) absent; (1) short (<10%); (2) long (>10%).
- 3) Relative angle of anterior horn: (0) in line with body axis; (1) continues dorsally; (2) continues ventrally; (3) absent.
- 4) Surface ornamentation of the carapace: (0) fine striae parallel to carapace margin; (1) fine striae oblique to carapace margin; (2) striae absent.
- 5) Placement of striae: (0) ventral and dorsal portions of carapace; (1) ventral portion of carapace only; (2) striae absent.
- 6) Striations of carapace: (0) parallel; (1) anastomosing; (2) absent.
- 7) Rim of carapace margin: (0) plain; (1) keel; (2) true doublure.
- 8) Spines of carapace margin: (0) absent; (1) present.
- 9) Extent of spines of carapace margin: (0) present on posterior margin only; (1) present on entire margin (other than dorsal) (2) absent.
- 10) Overall shape of the carapace: (0) subovate, elliptical; (1) subquadrate; (2) ovate.
- 11) Length to depth ratio of carapace: (0) narrow (>2.0) (1) intermediate (1.5–1.8) (2) deep (1.2–1.4).
- 12) Tuberculation of posterior portion of carapace: (0) not tuberculate; (1) sparsely or weakly tuberculate; (2) densely tuberculate.
- 13) Posterior margin of the carapace: (0) sinuous; (1) linear; (2) convex; (3) concave.
- 14) Angle of posterior margin of carapace: (0) perpendicular to body axis; (1) oblique to body axis.
- 15) Posteroventral spine: (0) absent; (1) present.
- 16) Posterodorsal spine: (0) absent; (1) present.
- 17) Nodes along the dorsal hinge: (0) 3, small and evenly spaced along the length of the carapace; (1) absent; (2) 3, clustered in the anterior region of the carapace.
- 18) Anteriodorsal region: (0) no marked difference in convexity; (1) markedly increased convexity.
- 19) Boundary of the anteriodorsal region: (0) broadly defined; (1) defined by distinct grooves.
- 20) Separation of nodes in the anteriodorsal region: (0) not well differentiated; (1) defined by distinct grooves.
- 21) Anterior tubercle ('optic node'): (0) absent; (1) present.
- 22) Number of well-defined anterior nodes: (0) none; (1) one to three; (2) five
- 23) Tubercles of anterior nodes: (0) absent; (1) present.
- 24) Centroventral lobe: (0) absent; (1) present.
- 25) Tubercles of centroventral lobe: (0) absent; (1) present.
- 26) Number of tubercles on dorsal lobe: (0) none; (1) one to four; (2) many.
- 27) Tuberculation of carapace margin: (0) absent; (1) present.
- 28) Cephalic carina: (0) absent; (1) present.

- 29) Nuchal carina: (0) absent; (1) present.
- 30) Lateral ridge located centrally on carapace: (0) absent (1) present (2) reduced.
- 31) Appearance of central ridge: (0) absent (1) smooth or punctata (2) tuberculate.
- 32) Shape of central ridge: (0) absent (1) linear (2) sigmoid (3) sinuous (with pronounced v in center).
- 33) Length of central ridge: (0) short (0–30 percent of carapace) (1) intermediate (40–70 percent of carapace) (2) long (75–100 percent or more of carapace).
- 34) Extent of central ridge: (0) absent (1) present only in the posterior region of the carapace (2) present only in anterior region of the carapace (3) present in both the anterior and posterior region of the carapace.
- 35) Central ridge extending anterior to centroventral region: (0) no; (1) yes.
- 36) Lateral ridge located 2/3 between ventral and dorsal edges of the carapace (dorsocentral ridge) (0) absent; (1) present.
- 37) Appearance of dorsocentral ridge: (0) absent; (1) smooth or punctate; (2) tuberculate.
- 38) Extent of dorsocentral ridge: (0) absent; (1) present only in the posterior region of the carapace; (2) present only in the anterior region of the carapace; (3) present in both the anterior and posterior region of the carapace.
- 39) Dorsocentral ridge extending to posterodorsal lobe: (0) absent; (1) present.
- 40) Dorsal ridge (present near the hinge line): (0) absent; (1) present.
- 41) Appearance of dorsal ridge: (0) absent; (1) smooth or punctate; (2) tuberculate.
- 42) Extent of dorsal ridge: (0) absent; (1) present only in the posterior region of the carapace (2) present in both the anterior and posterior region of the carapace.
- 43) Dorsal ridge extending to posterodorsal lobe: (0) absent; (1) present.
- 44) Ventral ridge (located between central ridge and ventral edge of carapace): (0) absent; (1) present.
- 45) Shape of rostrum: (0) ovate; (1) lanceolate; (2) absent.
- 46) Carina of rostrum: (0) absent; (1) one, median; (2) two, lateral.
- 47) Length of hinge line: (0) long (90–100 percent carapace length) (1) short (60–80 percent carapace length).
- 48) Median dorsal plate: (0) absent; (1) present.
- 49) Width of the median dorsal plate: (0) absent; (1) narrow (10–20 percent length) (2) broad (30–40 percent length).
- 50) Median carina of median dorsal plate: (0) absent; (1) present but smooth or punctate; (2) present with a row of spines or tubercles.
- 51) Ornamentation of median dorsal plate other than median carina: (0) absent; (1) chevron shaped lineations.
- 52) Surface of the abdominal segments: (0) smooth; (1) tuberculate.
- 53) Tubercles in defined rows on abdominal segments: (0) absent; (1) present.
- 54) Lateral spines of the abdominal segments: (0) absent; (1) present.
- 55) Striations of the abdominal segments: (0) present; (1) absent.
- 56) Orientation of abdominal striations: (0) largely longitudinal (axial) (1) largely perpendicular to axis; (2) oblique; (3) absent.
- 57) Scales of abdominal segments: (0) absent; (1) present.
- 58) Extent of abdominal scales: (0) present on all abdominal segments; (1) present on posterior segments only; (2) few scales, present on segment shoulder; (3) absent.

- 59) Relative lengths of telson and furcal rami: (0) telson longer; (1) equal length; (2) furcal rami longer.
- 60) Furcal rami: (0) thin and rod-like; (1) broad and spatulate; (2) absent.
- 61) Lateral spines of the telson: (0) absent; (1) present.
- 62) Surface ornamentation of the telson: (0) none; (1) tubercles; (2) lineations in a chevron pattern.
- 63) Furcal rami striae: (0) absent; (1) present.
- 64) Dorsal axial carina of telson: (0) absent; (1) present.
- 65) Ratio of A7:A6: (0) short (< 2.0) (1) long (≥ 2.0).
- 66) Ratio of telson:A7: (0) short (< 1.6) (1) long (≥ 1.6).

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